U. S. F. W. S. Research Report
#56
#56

LIMNOLOGY OF YELLOWSTONE LAKE IN RELATION TO THE CUTTHROAT TROUT

LIBRARY
MAY 4 1962
FISH & WILDLIFE SERVICE

UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
BUREAU OF SPORT FISHERIES AND WILDLIFE
RESEARCH REPORT 56

RESEARCH REPORTS

This series of reports was begun when the Fish and Wildlife Service was established in 1941; the series superseded Wildlife Research Bulletins of the Bureau of Biological Survey and Investigational Reports of the Bureau of Fisheries, those two bureaus having merged to form the Service. The Research Reports are being continued (with Research Report 54) in a slightly changed format, as the research-reporting series of the Bureau of Sport Fisheries and Wildlife (U.S. Fish and Wildlife Service), comprising reports of scientific investigations related to the work of the Bureau. The Bureau distributes these reports without charge to official agencies, to libraries, and to researchers in fields related to the Bureau's work; additional copies may usually be purchased from the Division of Public Documents, U.S. Government Printing Office.

Current Research Reports are—

54. Fluctuations in Age Composition and Growth Rate of Cutthroat Trout in Yellowstone Lake, by Ross V. Bulkley. 1961. 31 pp.

55. Mortality Studies on Cutthroat Trout in Yellowstone Lake, by Orville P. Ball and Oliver B. Cope. 1961. 62 pp.

56. Limnology of Yellowstone Lake in Relation to the Cutthroat Trout, by Norman G. Benson. 1961. 33 pp.

57. Chemical Composition of Blood of Smallmouth Bass, by Eddie Wayne Shell. In press.

58. Chronic Effects of Endrin on Bluntnose Minnows and Guppies, by Donald Irvin Mount. In press.

LIMNOLOGY OF YELLOWSTONE LAKE IN RELATION TO THE CUTTHROAT TROUT

Norman G. Benson

Fishery Research Biologist

RESEARCH REPORT 56

UNITED STATES DEPARTMENT OF THE INTERIOR

Stewart L. Udall, *Secretary*

Frank P. Briggs, *Assistant Secretary for Fish and Wildlife*

FISH AND WILDLIFE SERVICE

Clarence F. Pautzke, *Commissioner*

BUREAU OF SPORT FISHERIES AND WILDLIFE

Daniel H. Janzen, *Director*

Published by the U.S. Fish and Wildlife Service • Washington • 1961
Printed at the U.S. Government Printing Office, Washington, D.C.

For sale by the Superintendent of Documents, U.S. Government Printing Office
Washington 25, D.C. - Price 40 cents

CONTENTS

	Page
Introduction	1
Geology	2
Weather and water levels	2
Morphometry	3
Methods	4
Lake currents	6
Water temperatures	9
Secchi disk transparency	10
Water chemistry	11
Bottom types	15
Aquatic plants	16
Plankton	17
Benthos	20
Vertical distribution of cutthroat trout	21
Food of cutthroat trout	22
Trout density and limnology	24
Biology of Yellowstone Lake	26
Summary	28
Literature cited	29
Appendix A—Points of release and recovery of drift bottles	32
Appendix B—Points of release and recovery of drift bottles	33

ABSTRACT

Limnological data collected from 1954 to 1959 on surface currents, bottom currents, temperatures, bottom soils, water chemistry, plankton, bottom fauna, and higher aquatic plants are related to the biology of the cutthroat trout, *Salmo clarki lewisi*, in Yellowstone Lake (Wyoming). The lake, formed on Eocene lava, is oligotrophic and low in dissolved solids. *Diaptomus shoshone*, *Daphnia shoedleri*, and *Conochilus unicornis* made up more than 90 percent of the macroscopic zooplankton by number. Upwelling in West Thumb was demonstrated by temperature stratification and conductivities. Plankton distribution and abundance were related to currents and water chemistry. Depth distribution, feeding, and movements of trout are related to food abundance. Trout less than 315 millimeters in total length are not caught readily because of their feeding habits and greater dispersal. There is evidence that the heavy trout harvest in the northern part of the lake allowed *Gammarus lacustris*, an important trout food, to become locally abundant.

LIMNOLOGY OF YELLOWSTONE LAKE IN RELATION TO THE CUTTHROAT TROUT

By Norman G. Benson, *Fishery Research Biologist*

Rocky Mountain Sport Fishery Investigations
Logan, Utah

Limnological studies on Yellowstone Lake (Wyoming) began in 1890 when Forbes (1893) described the common zooplankters, noted their relative abundance, and recorded other general features of the lake. Except for occasional records of water temperatures and a few plankton collections, the lake was not studied limnologically again until 1954, when the staff of the Rocky Mountain Sport Fishery Investigations initiated the work reported here.

Much has been published on the biology of the cutthroat trout in Yellowstone Lake and tributaries (Cope, 1956, 1957; Ball, 1955; Laakso and Cope, 1956; Ball and Cope, 1961). The purpose of this paper is to describe general features of the lake ecology and to relate this information to the known life history of the cutthroat trout.

Orville Ball, Martin Laakso, and several fishery aids mapped the lake and collected some field data. Identification of zooplankters and bottom organisms was by Marvin Meyer, Alan Stone, W. W. Wirth, A. W. Bell, and Clarence Shoemaker; Arthur Holmgren identified the higher aquatic plants. I appreciate the critical review of the manuscript by Oliver B. Cope, C. J. D. Brown, W. T. Edmundson, and Ross V. Bulkley.

The fish fauna of Yellowstone Lake includes the cutthroat trout, the longnose sucker *Catostomus catostomus* (Forster), the longnose dace *Rhinichthys cataractae* Valenciennes, the smallfin redside shiner *Richardsonius balteatus hydrophlox* (Cope), and the lake chub *Hybopsis plumbea* Agassiz. Only cutthroat trout and longnose suckers are found throughout the lake. The other species are restricted to shallow lagoons in the northern end and West Thumb (fig. 1), to very shallow (less than 2 meters deep) protected littoral zones of the lake, or to tributary streams. The original fish fauna included only the cutthroat trout and the longnose dace.

Information is presented on lake geology, lake morphometry, weather, water levels, bottom currents, surface currents, temperatures, bottom soils, water chemistry, phytoplankton, zooplankton, food of trout, and depth distribution of trout. A discussion of the relations of these conditions to the biology of the cutthroat trout in the lake follows.

GEOLOGY

The watershed of Yellowstone Lake has been an area of volcanic activity since the Eocene period, when large amounts of volcanic breccias were deposited (Bauer, 1955). With another heavy breccia deposit in the middle Cenozoic era, the whole series of breccias formed a stratum about 2,000 meters thick. Rhyolite deposits were superimposed on the breccias in certain areas in the late Cenozoic. The original breccias are exposed on the southern and eastern drainage basins of Yellowstone Lake, and rhyolite deposits are exposed on the south shore and in the western drainage area. Small deposits of dolomite, basalt, and glacial drift are present in isolated sections of the watershed.

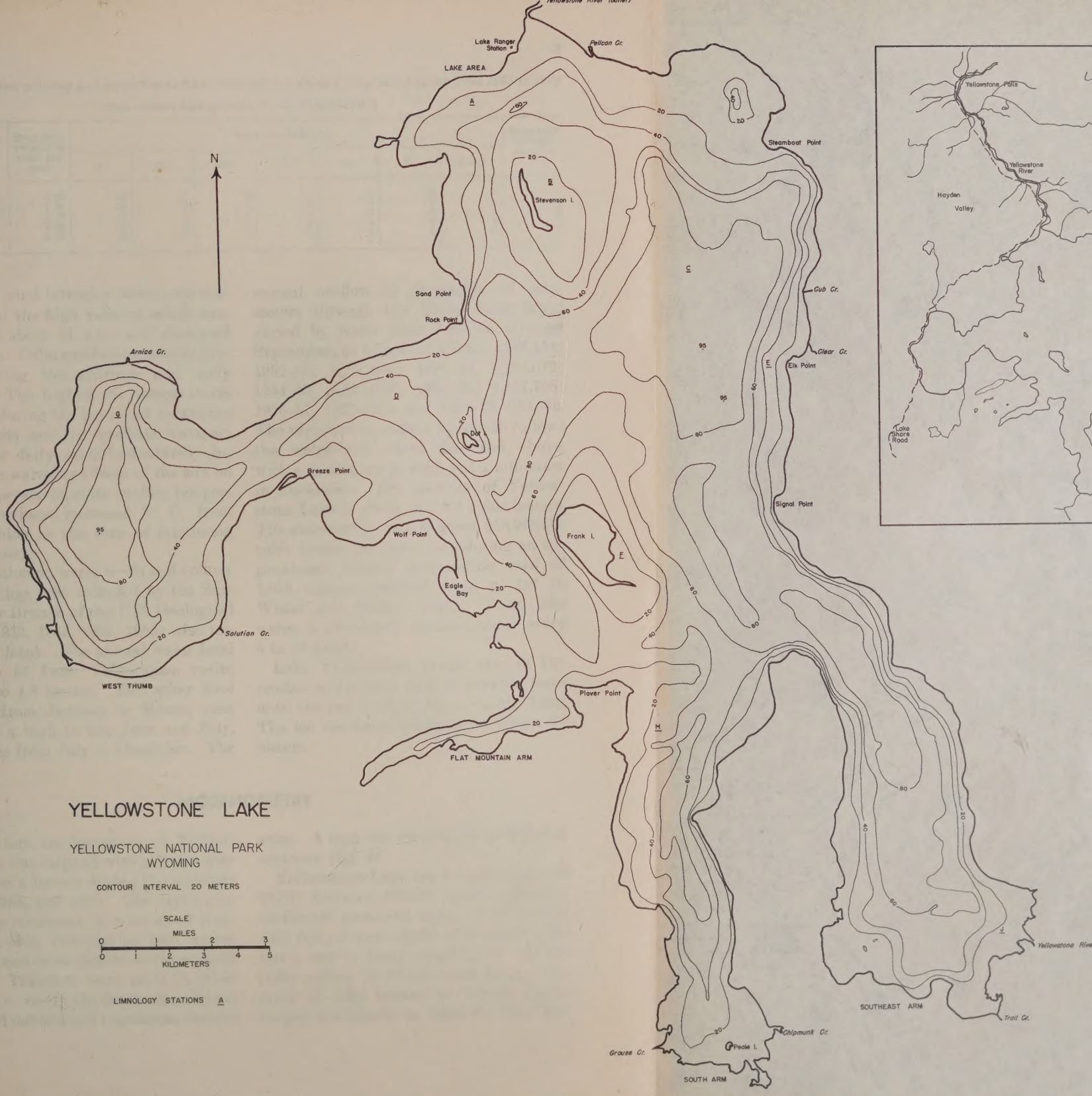
The available information does not allow an adequate explanation of the geological formation of the present basin of Yellowstone Lake, although the original lake basin was believed to have been formed by a subsidence or readjustment of the original lava flows in the Eocene. Bauer also mentions the possibility that pre-Eocene glaciation may have formed the original basin. Recent glaciation, erosion, and milder forms of volcanic activity have sculptured the present basin. Many active geysers and hot springs are in the watershed. The West Thumb area is considered to be an old geyser basin, and hot springs are still present on the shoreline and below the water surface.

During its geological history, the lake has drained into three oceans. Until the early Pleistocene, the lake drained into the Pacific Ocean via the Snake River. At that time the Grand Canyon of the Yellowstone formed, and the lake drained northward into Hudson Bay. Since the retreat of the glaciers, the lake has drained through the Missouri River system into the Gulf of Mexico. During the glacial period, the lake was much larger than at present, owing to a glacial lobe at the present site of the Grand Canyon of the Yellowstone (fig. 1). Several lake terraces from the glacial period can be observed in Hayden Valley. One lake terrace has a present elevation of 2,470 meters, or 112 meters higher than the lake altitude.

WEATHER AND WATER LEVELS

The lake watershed is on the east slope of the Continental Divide at an altitude of 2,358 meters (7,731 feet). Air temperatures, wind measurements, and precipitation for the Yellowstone Lake area have been collected at the Lake Ranger Station for the U.S. Weather Bureau. The mean monthly temperatures from 1953 to 1957 ranged from minus 15.3° C. (4.5° F.) in February 1956, to 16° C. (60.8° F.) in July 1954. The mean monthly temperature during most summer months averaged about 13° C. (55.4° F.), and during winter months averaged minus 9.5° C. (14.9° F.). Air temperatures in the summer rarely reach 30° C. (86.0° F.). The annual precipitation from January 1953 to November 1957 varied from 39.3 cm. (15.49 inches) in 1953 to 62.2 cm. (24.47 inches) in 1955. Most precipitation falls during the late fall and winter months in the form of snow.

Data collected at the Lake Ranger Station on wind velocity and direction showed that the predominant winds were from the south and southwest (table 1), and that wind velocities were higher when the wind came from the latter two directions. Winds were stronger in 1955, 1956, and 1959 than in 1957 and 1958. Diurnal



595956 O - 62 (Face p. 2)

FIGURE 1.—Contour map of Yellowstone Lake showing limnology stations and localities mentioned in the report.

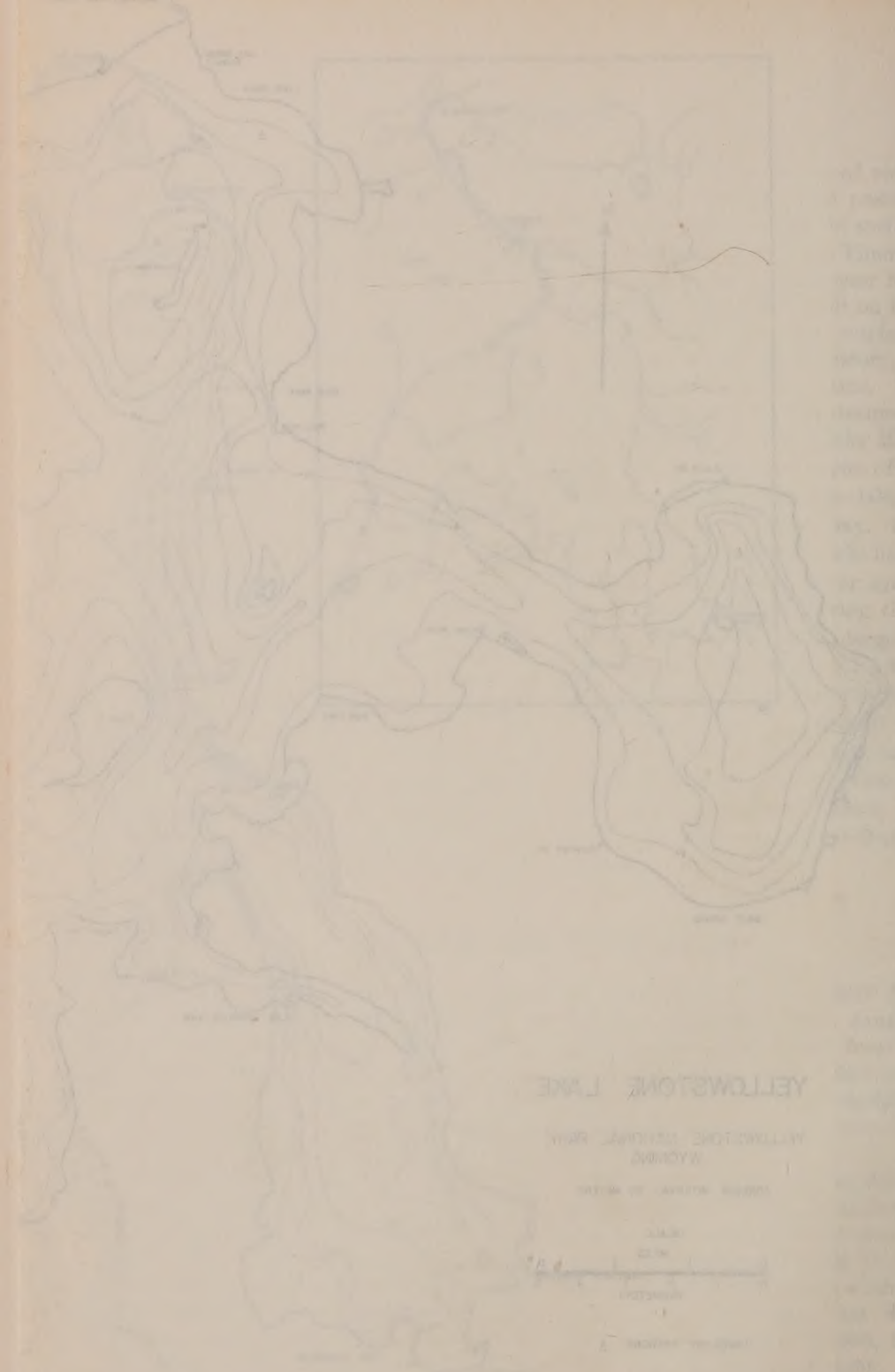


TABLE 1.—*Wind velocity and direction at Lake Yellowstone during July and August from 1955 to 1959*

[Data collected daily at 4 p.m., at Lake Ranger Station]

Year	Mean daily velocity in miles per hour	Days recorded from—							Days with no wind recorded
		S.	SW.	SE.	E.	N.	W.	Other	
1955	5.92	25	17	4	1	0	10	0	5
1956	7.04	24	18	1	2	4	6	7	0
1957	1.35	21	4	1	4	2	0	2	28
1958	2.30	23	6	8	5	2	3	8	7
1959	8.05	28	18	2	0	5	5	4	0

changes in wind intensity were quite regular in that the high velocity winds usually began about 11 a.m. and decreased about 5 p.m. Calm conditions usually prevailed during the evenings and early morning. The highest air temperatures prevailed during the period of maximum wind velocity and the resultant wave action. This daily cycle undoubtedly increased the warming effects of the sun on water temperatures, since surface temperatures sometimes increased 3° C. from early morning to the time of maximum wind intensity.

Information on water levels and volume of outflow has been collected by the Surface Water Branch of the U.S. Geological Survey (1952, 1953, 1954, 1955; also unpublished data). The annual water level fluctuation of Lake Yellowstone varies from 1.5 to 1.8 meters. The water level is lowest from January to March, rises rapidly to a high in late June and July, and recedes from July to December. The annual outflow in thousands of cubic meters through the Yellowstone River varied by water year, October through September, as follows: 1951–52, 1,386,454; 1952–53, 1,270,505; 1953–54, 1,284,073; 1954–55, 1,003,674; 1955–56, 1,587,798; 1956–57, 1,270,949; and 1957–58, 939,482. The variation in outflow by month follows the water-level curve described above, with a maximum in July and a minimum in December. The capacity of Yellowstone Lake is about 14×10^9 cubic meters. The evaporation rate is about 358,948,500 cubic meters per year, considering an approximate annual evaporation rate of 1.016 meters (derived from p. 151 in Wisler and Brater, 1949). Thus, lake water is completely replaced about every 8 to 10 years.

Lake Yellowstone freezes over in December or January, and ice does not leave until the last week of May or early June. The ice reaches a thickness of 0.4 to 0.9 meters.

MORPHOMETRY

The bottom configuration of Yellowstone Lake was mapped with a fathometer mounted on a launch during the summers of 1954, 1955, and 1956. The depth contours were measured by a series of transects at 1-mile intervals in both north-south and east-west directions throughout the lake. Transects were made in other directions to verify the depths determined by the grid method and to measure various arms. A map was constructed to 20-meter contours (fig. 1).

Yellowstone Lake has a surface area of 35,391 hectares (136.66 square miles), a maximum measured depth of 98 meters (320 feet), a mean depth of 42 meters (139 feet), and a basin capacity of 14×10^9 cubic meters (12,095,264 acre feet). The areas of lake bottom at various depth ranges are shown in table 2. The lake

basin has a deep trench along the east shore which extends into both the South Arm and Southeast Arm. It extends westward between Stevenson and Frank Islands to a point near the west shore of the main body of the lake. The lake basin in West Thumb is more cone-shaped, with no islands and with the deepest area in the approximate center of the thumb.

The lake is shaped like a hand with three fingers and a thumb, and has a shoreline development of 3.04. The watershed has an estimated area of 261,590 hectares (1,010 square miles) and consists principally of lodgepole pine forest and alpine meadows. The largest stream entering the lake is the upper Yellowstone River, but the lake cannot be considered simply an enlarged section of the river, since 42.2 percent of the lake watershed is outside the upper Yellowstone River drainage.

TABLE 2.—*Areas of various depth ranges in Yellowstone Lake*

Depth range	Area, in—			Percent of total
	Square miles	Acres	Hectares	
Less than 20 meters	31.44	20,121	8,143	23.01
20–40 meters	34.82	22,282	9,017	25.48
40–60 meters	26.70	17,088	6,916	19.54
60–80 meters	26.40	16,893	6,837	19.32
80–95 meters	17.29	11,066	4,478	12.65
Total area of lake	136.65	87,450	35,391	

METHODS

Limnological stations.—Originally, in 1954, 20 stations were established for measuring physical and biological conditions. In 1957 the number was reduced to 10 because it was found that variations in the lake could be accurately determined from the 10 stations shown on figure 1.

Temperature and surface currents.—Temperatures were measured by a bathythermograph (depth range, 61 m.) which was calibrated periodically with a resistance thermometer. Temperatures below 61 meters were collected with a reversing thermometer. For describing water stratification, the metalimnion as defined by Hutchinson (1957) has been used to define the whole region in which the temperature gradient is steep.

Surface currents were determined by releasing 340 drift bottles on 16 different seeding lines in the lake. The bottles were designed by the Great Lakes Biological Laboratory (Johnson, 1958). These bottles were found to resist wind action unless surface currents were produced by wind. To facilitate recovery, our bottles were painted red by swirling thinned paint on the inside. The bottles were released while maintaining a launch at a constant speed and releasing the bottles at constant time intervals. Bottles were recovered, and their locations noted, by National Park Service employees, tourists, and U.S. Fish and Wildlife employees.

Bottom currents. — Bottom currents were measured by a modification of the leaning-tube-type current indicator described by Carruthers (1958a and 1958b). The indicator (fig. 2) proved accurate enough to measure current speeds to the nearest tenth of a knot and to measure direction to within 20 degrees. The graph illustrated by Carruthers (1958b) was used for recording current speed, since it was found that our modification of his bottle followed this curve the same as a bottle constructed to his specification.

Water chemistry.—Standard Methods for the Examination of Water, Sewage, and Industrial Wastes (U.S. Public Health Association, 1955) was used as a guide for dissolved-oxygen, free-carbon-dioxide, and alkalinity determinations. Oxygen values were corrected for temper-

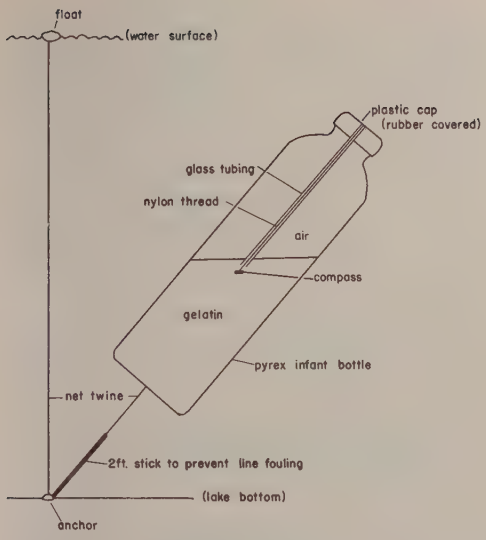


FIGURE 2.—Diagrammatic sketch of bottom-current indicator.

ature and altitude from the nomograph in Hutchinson (1957). Specific conductance was determined by a conductivity bridge and readings were converted to a standard 25° C. A more complete chemical analysis of four water samples was conducted by the Surface Water Branch of the U.S. Geological Survey.

Secchi disk transparency.—A Secchi disk (20 cm. in diameter, black and white) was used to measure the limit of visibility, and a water telescope was utilized to eliminate surface glare.

Bottom soils.—Five bottom-soil samples were analyzed for chemical properties by the Soils Laboratory of Utah State University. The percentage of organic matter in 59 additional samples was determined by the laboratory. Observations were made on the distribution of boulders, rubble, silt, sand, and other bottom types in different sections of the lake.

Plankton.—Net plankton tows were made with a Wisconsin plankton net using No. 25 bolting cloth during 1956. This method sampled the top 10-meter stratum of water and the net strained an estimated 211 liters (10.99 cu. ft.) of water. Several inherent errors in this method (as summarized by Welch, 1948) are recognized. The samples were preserved in a 3-percent solution of formaldehyde.

In 1957 and 1958 water for net plankton analyses was collected with a 3-liter Kemmerer water sampler. Each sample consisted of 10 liters of water and was strained through a plankton net with No. 25 bolting cloth. Plankton samples for phytoplankton measurements were counted in a Sedgewick-Rafter counting cell under a magnification of 100×. For zooplankton analyses, samples were counted with a rotary-type counter under a dissecting microscope at a magnification of 30× (Ward, 1955). Data on phytoplankters are weak because many forms pass through No. 25 bolting cloth. Only abundant zooplankters were identified to species.

Bottom organisms.—Bottom samples were collected with a 6- by 6-inch (231 sq. cm.) Ekman dredge, and the organisms were separated from the bottom soils by sieving through a No. 30 Tyler (0.589 mm.) screen. Four samples were collected at each station. Sandy or rocky bottoms could not be sampled adequately with the Ekman dredge, although we determined the type and relative abundance of organisms in these bottom types by taking several dredge samples. Common forms were identified to species by specialists.

Stomach analyses.—Stomachs for food contents were collected from anglers by creel-census clerks in 1957 and 1958. Additional stomachs were collected with gill nets in 1957 and 1958. All were preserved in formalin and sorted in the laboratory. Organisms were identified as closely as possible and counted. Aliquots were used in counting large samples.

Gill netting.—Experimental gill nets (125 by 6 ft.) with square meshes 2½, 2, 1½, 1, and ¾ inches were used for sam-

595956 O - 62 - 2

pling fish in different sections of the lake at different depths. All nets were set from 3 to 6 p.m. on one day and picked up from 8 to 10 a.m. the following morning. Each set is considered to be an equal sample of an overnight set.

Areas of lake.—Three areas of the lake have been differentiated for purposes of comparing lake limnology with movements of trout and fishing pressure intensity. The West Thumb area consists of the lake west of a line between Rock Point and Wolf Point and includes 19.1 percent of the lake area (see fig. 1). The northern area consists of all of the lake north of a line between Rock Point and Elk Point and includes 25.4 percent of the area. The southern area consists of all the lake south and east of these lines and includes 55.5 percent of the area.

Catch of fish.—Creel census data were collected on Yellowstone Lake from 1950 to 1959 and the method has been described (Moore, et al., 1952). The catch each year was computed from sampling different segments of the fishery, such as shore fishermen, guide boats, and private boats. All of the fishing in each segment of the creel census was done predominantly in a certain area. It was thus possible to determine with some accuracy the total catch each year as coming from each of the three areas of Yellowstone Lake. The West Thumb harvest includes all rowboats and guide boats from West Thumb, 20 percent of the trailer-boat catch, and 25 percent of the shoreline catch. The catch from the southern area consisted of 75 percent of the cruiser catch, 15 percent of the trailer boat catch, and 5 percent of the catch from Lake or Fishing Bridge guide boats. All remaining fish caught were taken in the northern area.

LAKE CURRENTS

Surface currents. — Certain considerations are necessary in the interpretation of drift bottle data:

1. Few bottles were recovered in the open water, and the route that a bottle followed from its release point to its destination was unknown. The predominant currents in the lake were deduced from a series of recoveries.

2. The number of bottles recovered on certain isolated southern sections of the lake shore was low owing to infrequent visits by tourists and National Park Service employees. Special efforts were made by our employees to collect bottles in these areas, but many undoubtedly were lost.

3. Descriptions of recovery points were rarely precise and no attempts were made to interpret minor differences in the general current patterns from a few unusual recovery points.

4. Complete analyses of the influence of daily wind direction on currents is not possible. The wind data includes readings at 4 p.m. at the Lake Ranger Station and experience has shown that these readings did not always reflect conditions for the entire lake or even for a complete day.

Our surface-current information is based on the recovery of 155 bottles from 340 released, or a recovery rate of 45.6 percent. A summary of the release points and recovery points is plotted in appendix figures 1 and 2. Surface currents as derived from these recoveries are shown in figure 3.

The surface currents on Yellowstone Lake during 1957 and 1958 flowed mostly toward the north, east, or northeast, and were caused by the predominant winds from the south and southwest (table 1). Occasional winds from the east or southeast had much less velocity than winds from the south or southwest. Most recoveries were made on the north and east shores of the lake. The only area where the currents regularly deviated from the above-mentioned directions was around Frank Island and at the entrance to West Thumb. Several bottles were carried from

seeding lines northwest of Frank Island (seeding lines *E* and *F* on appendix tables 1 and 2) into West Thumb and southeast of Frank Island. Most of the bottles that were released within West Thumb were collected on the north and northwest shores of the main body of the lake, pointing to the large amount of surface water leaving Thumb Lake. Surface water in the South and Southeast Arms also was carried northward, although many bottles were recovered on the east shores of these arms.

The current speed can only be approximated, but one bottle traveled a minimum of 7 miles in 1 day. Several bottles were collected after being carried 10 miles in 2 days.

Bottom currents.—Bottom currents were measured at 57 stations from August 20 to September 7, 1959, and the results plotted on figure 4. The following general conclusions were deduced from these measurements:

1. Some water flows along the lake bottom into West Thumb.
2. Currents southwest of Frank Island were variable, but flowed generally to the northeast.
3. Currents in the northeast main body of the lake flowed northward along the east shore and westward along the north shore.
4. There was evidence of clockwise bottom current circulation within West Thumb.

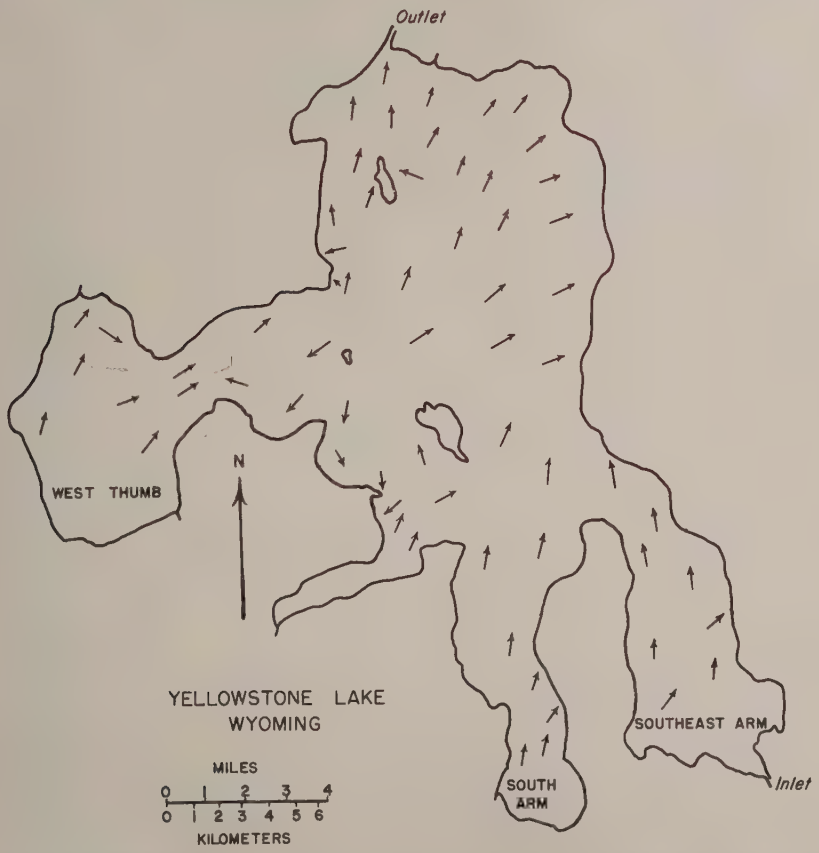


FIGURE 3.—Direction of surface currents on Yellowstone Lake as deduced from drift-bottle recoveries shown in appendix figures *A* and *B*.

5. No consistent relation was found between depth and current speed.

Relations between surface and bottom currents.—The predominant north and northeasterly flow of surface water in Yellowstone Lake is generally compensated by a northwesterly and southwesterly flow of water along the lake bottom. The great mass of water that piles up on the east shore of Yellowstone Lake forces bottom currents to flow in northerly and westerly directions, and bottom currents continue to flow westward back into West Thumb section. The bottom-current circulation in West Thumb suggests a clockwise movement. Mixture of bottom and surface water probably occurs in West Thumb as evidenced from our temperature and water-chemistry information presented later. Undoubtedly the subsurface current patterns described above are an oversimplication of the currents actually occurring in Yellowstone Lake, although our data do not allow a more complete description of the true conditions. Mortimer (1952) described the occurrences of internal seiches in Windemere, and both our current and temperature data (presented later), when compared with Mortimer's data, suggest similar conditions in Yellowstone Lake. This is true especially in the region from West Thumb to the northeast shore where the movement of surface water is most pronounced.

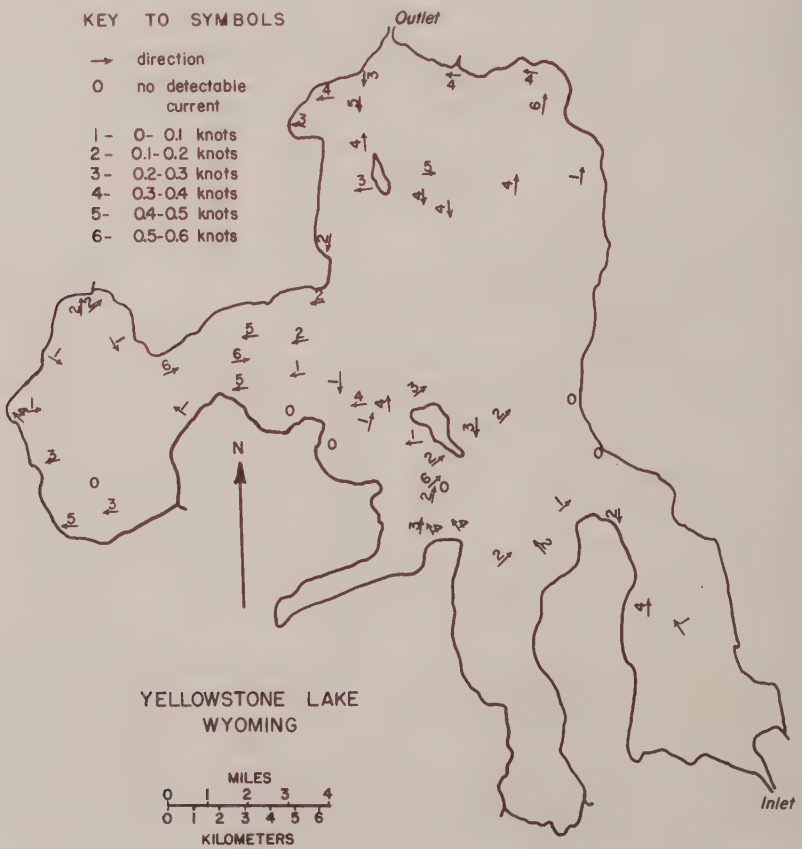


FIGURE 4.—Measurements of bottom currents in Yellowstone Lake from August 20 to September 7, 1959.

WATER TEMPERATURES

Water temperatures at different depths in Yellowstone Lake have been measured from June to the middle of October. Data from Station A have been used for illustrating seasonal and annual differences because it is north of the area of greatest surface water movement and the most complete data have been collected at this station (fig. 5). After the ice leaves near the end of May or in early June, the lake begins to warm, but remains virtually homothermous (4.5 to 5.8° C.) during early June. This period is comparable to the early spring warming period described by Church (1945) for Lake Michigan. In late June the surface water begins to form a protective warmer layer, although no clear-cut metalimnion has yet formed. At this time several temporary metalimnion layers have been observed (see June 30, 1959, in fig. 5), as has been recorded by Pennak (1955) from Grand Lake, Colorado. Surface temperatures reach between 10.0 and 14.0° C. during this phase.

In middle July a permanent metalimnion begins to form and the temperature gradient in the epilimnion narrows down to about 10° C. The depth of the epilimnion during its early formation usually varies from 5 to 10 meters. During late July and early August the stratification becomes complete and the summer stagnation period described by Church begins. Surface temperatures recorded during this period varied from 15.5 to 17.8° C., while the total temperature drop in the epilimnion was usually less than 4° C. The temperature gradient in the metalimnion varied from a drop of 12° C. in 10 meters to 10° C. in 3 meters. Temperatures below 90 meter depths during complete stratification were not recorded below 4.6° C., which is the temperature reached before stratification.

In late August the lake surface water begins to cool and the metalimnion starts to sink. This latter layer develops a smaller temperature range and the temperature gradient decreases. Temperatures in September at 30 meters were higher than in August, due to the sinking of the metalimnion. On October 15, 1958,

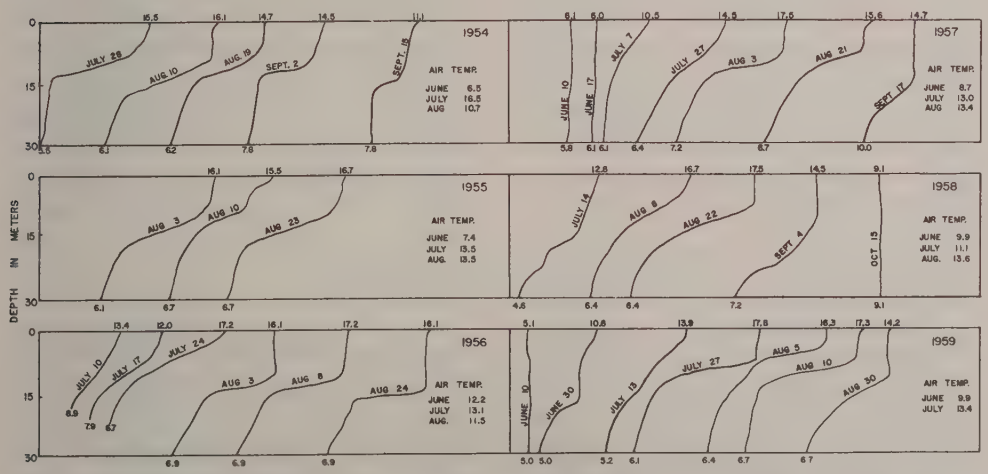


FIGURE 5.—Water temperatures (°C.) to 30 meters off Lake Area from 1954 to 1959. Mean monthly air temperatures each year included.

595956 O - 62 - 3

the surface temperature was 9.1° C. and a slight metalimnion was still present from 32 to 35 meters.

Differences in time of stratification among years appeared to be related to mean monthly air temperatures in June and July, shown on figure 5. Comparable data for 1956 and 1959 both showed earlier complete stratification than other years, and the mean air temperatures for these months were higher than recorded during other years.

A comparison of the water levels of Yellowstone Lake from 1954 to 1959 (table 3) with temperature stratification suggests that the thickest epilimnion strata formed in August during the years of high water such as 1954, 1956, and 1957. High water levels in 1959 were not, however, associated with a deep epilimnion. All years of high water showed a more abrupt temperature gradient in the metalimnion than the years of low water levels. This condition is possibly caused by the heavier stream runoff during high water level years, since stream temperatures reach either close to or above epilimnion temperatures soon after the first heavy runoff period in early July, and stream water, therefore, remains in and increases the depth of the epilimnion layer. The data suggest that Yellowstone Lake circulates twice a year and is a first-class dimictic lake, as classified by Hutchinson (1957).

TABLE 3.—*Mean monthly water levels in Yellowstone Lake during June, July, August, and September, 1954 to 1959*

[In meters above the datum of 2,357.48 meters. Date collected by U.S. Geological Survey, 1952, 1953, 1954, and 1955, and unpublished data]

Year	June	July	August	September
1954	1.31	1.58	1.03	0.64
1955	1.07	1.24	0.90	0.57
1956	1.83	1.59	1.03	0.66
1957	1.37	[1] 1.44	[1] 0.97	0.63
1958	1.07	1.07	[1] 0.75	[1] 0.50
1959		1.44	0.95	

[1] Data not complete.

Striking differences were evident between the thermal stratification patterns in the West Thumb area and in the east central part of the lake. West Thumb had a thin epilimnion and an indistinct metalimnion, while the north central section had a thick epilimnion and a very distinct metalimnion (fig. 6). Intermediate conditions existed at the neck of West Thumb and in other sections of the lake. These conditions were caused by the predominant winds from the south and southwest. Data from drift bottles showed that surface water is moved from West Thumb to the central and north central parts of the lake. This water movement probably caused an upwelling in West Thumb and a piling up of surface water in the eastern part of the lake. Miller (1952) and Ayers and associates (1958) observed conditions similar to this in certain windy areas of the Great Lakes.

SECCHI DISK TRANSPARENCY

Readings with a Secchi disk during August, 1957 and 1959, varied from 6.5 to 8.3 meters on overcast days and from 8.8 to 10.1 meters on clear days. Variations among different stations in the lake were not consistent and were not always related to plankton abundance. These readings were greater than those recorded by Pennak (1955) for mountain lakes in Colorado, even though all were collected during the August pulse of *Anabaena* or the period of lowest transparency.

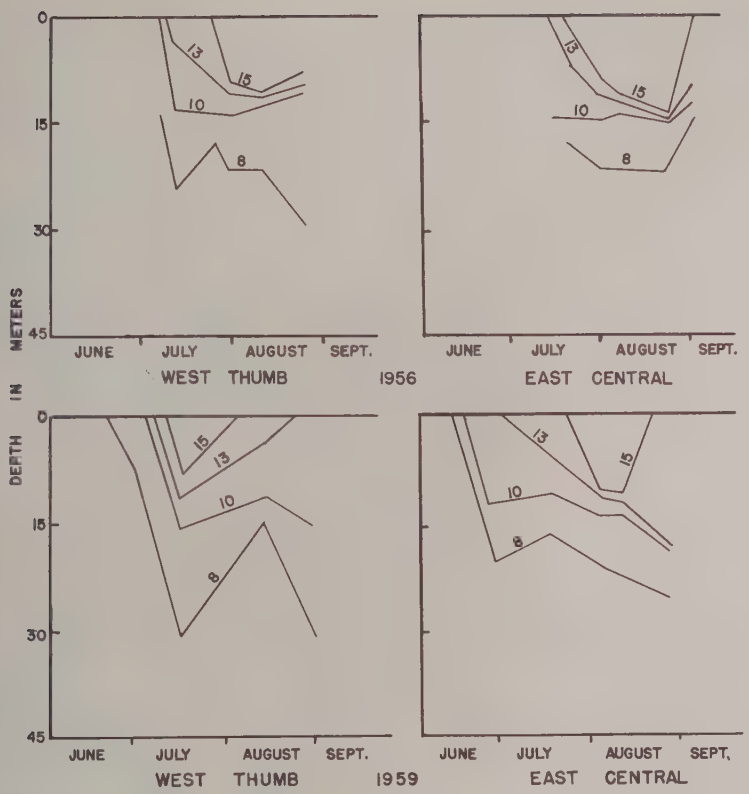


FIGURE 6.—Depths of isotherms (°C.) in West Thumb (station G) and the east central part of Yellowstone Lake (station C) during 1956 and 1959.

WATER CHEMISTRY

Yellowstone Lake is located approximately on the Continental Divide and drains a watershed of igneous rocks of volcanic origin. The chemical composition of the water is "primitive" in the sense that it has not been altered by civilization, and it does not drain sedimentary rocks.

Ionic composition.—The ionic composition of the water classifies it as the bicarbonate type, as defined by Rodhe (1949) (table 4). By arranging the major electrolytes into milliequivalents which presents their reacting weight, major anions exist in the order of HCO_3, SO_4, Cl. The major cations exist in the order Na, Ca, Mg, K, which is indicative of soft water draining igneous rocks. This ionic composition is similar to North German soft-water lakes summarized by Ohle (1955).

Bicarbonates ranged from 33 to 35 mg./l. while most ionic concentrations were relatively low. Several differences were apparent from a comparison of ions from the four sections of the lake. In general, West Thumb water had the highest values of Ca, Mg, Na, K, Cl, F, and B. Concentrations near the outlet and east of Stevenson Island were similar to each other and the lowest values were in the Southeast Arm. The higher values in West Thumb are due both to an upwelling

TABLE 4.—*Chemical analysis of water collected from 2 to 10 meters at four stations in Yellowstone Lake on July 28, 1958*

[Analyses by U.S. Geological Survey. Milliequivalents per liter (me./l.) presented for major cations and anions]

Constituents	Analysis of water collected in—							
	Middle Southeast Arm		Middle West Thumb		Four miles east of Stevenson Island		Near outlet	
	mg./l.	me./l.	mg./l.	me./l.	mg./l.	me./l.	mg./l.	me./l.
SiO_2	7.4		7.2		5.6		5.7	
Fe	0.02		0.01		0.02		0.02	
Ca	4.5	0.2245	5.0	0.2495	4.9	0.2445	4.5	0.2245
Mg	2.4	.1974	2.6	.2138	2.4	.1974	2.4	.1974
Na	8.0	.3478	9.4	.4087	9.1	.3957	8.9	.3870
K	1.8	.0460	2.0	.0512	1.5	.0384	1.7	.6435
HCO_3	33	.5408	35	.5737	35	.5737	34	.5573
SO_4	8.0	.1666	8.0	.1666	9.8	.2040	7.8	.1624
Cl	4.4	.1241	5.6	.1579	4.6	.1297	4.8	.1354
F	0.5		0.6		0.5		0.5	
NO_3	0.2		0.1		0.1		0.1	
B	0.08		0.13		0.09		0.10	
Specific conductance (25° C.)	86.3		96.4		92.2		93.2	
pH	6.8		6.8		6.7		7.0	
Dissolved solids residue on evaporation at 180°C	54		57		55		55	
Hardness	21		23		22		21	

influence caused by south and southwesterly winds and possibly to hot spring activity on the west shore and below the water surface in West Thumb. Water from hot springs is rich in SiO_2, CO_2, Na, and Cl. Hot spring water would presumably rise to the surface immediately, and any influences would be recorded in our sampling. Upwelling water was considered to be of greater importance, however, because data presented later on conductivities indicated the increase in ionic concentrations was related to the clockwise circulation in West Thumb and not to the principal locality of hot spring activity in the extreme west end of the Thumb. Also, there is no evidence of local hot spring influence in the reading from the outlet where Pelican Creek contributes much water from hot springs. Higher SiO_2 in the Southeast Arm is believed to be due to the inflow of the Yellowstone River.

Conductivities.—Water conductivity is directly related to total dissolved solids or total ion concentration. Conductivities from various stations at 5 and 10 meters (epilimnion) in Yellowstone Lake showed that West Thumb usually showed the highest readings, while Southeast Arm showed the lowest readings (table 5). In general, the northern part of the lake showed higher readings than the southern section. The pattern of water circulation probably causes this condition. The monthly changes from July to September were not consistent at any station, although the highest epilimnion readings were usually recorded immediately after complete thermal stratification. In 1957 this occurred in early July and in 1959 it occurred in late June.

Conductivities usually increased with depth, but not consistently so (table 6). The stations which were most influenced by the summer water circulation, such as West Thumb, east of Dot Island, and Elk Point, showed maximum readings in mid-August. Those protected stations, such as east of Frank Island and in South Arm had minimum readings in August. The epilimnion layers were more shallow (6–8 m.) in the protected stations than in the exposed stations (12–15 m.), and it is reasonable to assume that a more concentrated trophogenic zone would use up nutrients more rapidly than a broad zone. Also, the mixture of surface and deep water in exposed stations would serve as a method of replenishment of nutrients.

TABLE 5.—*Conductivities (25° C.) in reciprocal megohms at different locations in Yellowstone Lake from 1957 to 1959*

[Dates of collection for each month below each year. Figures represent average of readings at 5- and 10-meter depths]

Location in lake	June		July			August			September			Means of readings by area
	1957 (June 20–25)	1959 (June 26–July 1)	1957 (July 2–10)	1958 (July 12–18)	1959 (July 14–22)	1957 (Aug. 19–23)	1958 (Aug. 6–14)	1959 (Aug. 10–13)	1957 (Sept. 15–18)	1958 (Sept. 3–4)	1959 (Aug. 30–Sept. 2)	
Off Lake area	101		94	91	85	104	89	88	90	91	84	92
Five kilometers east of Stevenson Island		84	103	86	91	101	89	57	63	91	92	86
Off Dot Island	95	87	115	90	91	103	99	98	105	89	88	96
Middle West Thumb	101	91	123		83	99		103	105	92	91	99
Off Frank Island	97	86	105	86	86	80	80	76	62	86	74	83
Mouth South Arm	101	86	101			78	93	76	64	86	75	84
Mouth Southeast Arm	85		77		72	75	86	97	63		93	81
Mean readings for period	97	87	103	88	85	91	89	85	79	89	85	

TABLE 6.—*Variations in conductivities (25° C.), in reciprocal megohms, collected during 1959 by depth (meters) and location*

Location of collecting point	June 26–July 1					July 29–August 3					August 10–13						
	10	15	30	46	61	10	15	30	46	61	0	15	30	46	61	76	89
Middle West Thumb	91	91	93	100	92	89	89	93	96	97		103	104	107	106		
East of Dot Island	88	96	90	94	95	86	85	89	88			98	108	105	98	103	
Off Elk Point	91	88	87	90	88	75	73				95	93	95	96	91	89	89
Ten kilometers east of Stevenson Island	84	88	87	97		73	78	79	79	78	87	87	89	91	91	91	105
Mid South Arm	86	91	88	86	88	88	88	89	89	88	76	75	76				
Five kilometers east of Frank Island	86	90	107	90		86	87				76	80	78	72	76	74	
Mean by depth and sampling period	88	91	92	93	91	83	83	88	88	88	84	89	92	94	92	89	97

The distribution of conductivities by depth in and near West Thumb was measured on July 29, 1959, to determine how surface and bottom current measurements were related to conductivities (fig. 7). The data clearly demonstrated a clockwise circulation with conductivities increasing from the south to the north section of the area. The accumulation of additional nutrients from subsurface waters or upwelling can account for the increase in nutrients as water circulates in West Thumb. The hot spring activity is concentrated in the western part of the thumb. Both hot springs and upwelling probably accounted for the increases in the western and northern stations.

Alkalinity. — Bicarbonate alkalinities measured during 1957 ranged from 22 to 41 mg./l., usually varying from 30 to 33 mg./l. The readings showed the same general seasonal, horizontal, and vertical distributions as conductivities.

Dissolved oxygen.—Theinemann (1928) showed that lake morphometry has a strong bearing on oxygen concentrations, and that large, deep lakes rarely develop deficits. In 1957 oxygen was measured at all stations of the lake from mid-June to mid-September, and most readings down to 60 meters were near saturation. Some seasonal measurements of oxygen concentrations as compared with saturation values are shown in table 7, which also presents the lowest dissolved oxygen reading recorded, that of 53 percent saturation on July 25, 1957.

TABLE 7.—*Some summer dissolved oxygen concentrations (DO) from Yellowstone Lake during 1957 and 1959, compared with saturation (S) values*

[Values in milligrams per liter and adjusted for altitude. Collected at stations A and B]

Depth	June 20, 1957		July 25, 1957		Aug. 20, 1957		Sept. 18, 1957		Sept. 10, 1959	
	DO	S	DO	S	DO	S	DO	S	DO	S
0 meters	10.0	9.5	7.4	7.7	7.2	7.2	7.8	7.3		
4.5 meters	10.0	9.5	7.4	7.8	7.2	7.3	8.2	7.5		
9 meters	10.2	9.6			8.0	7.2	8.0	7.5		
15 meters									8.5	8.8
20 meters	9.8	9.7					8.4	7.9		
22 meters			8.3	8.6	8.3	8.3			8.3	9.2
30 meters	9.6	8.9			8.3	8.6			8.0	9.3
45 meters			4.9	9.2	8.3	8.7			8.7	9.2
60 meters					8.2	9.3			8.2	9.3
76 meters									8.0	9.5
92 meters									6.2	9.5

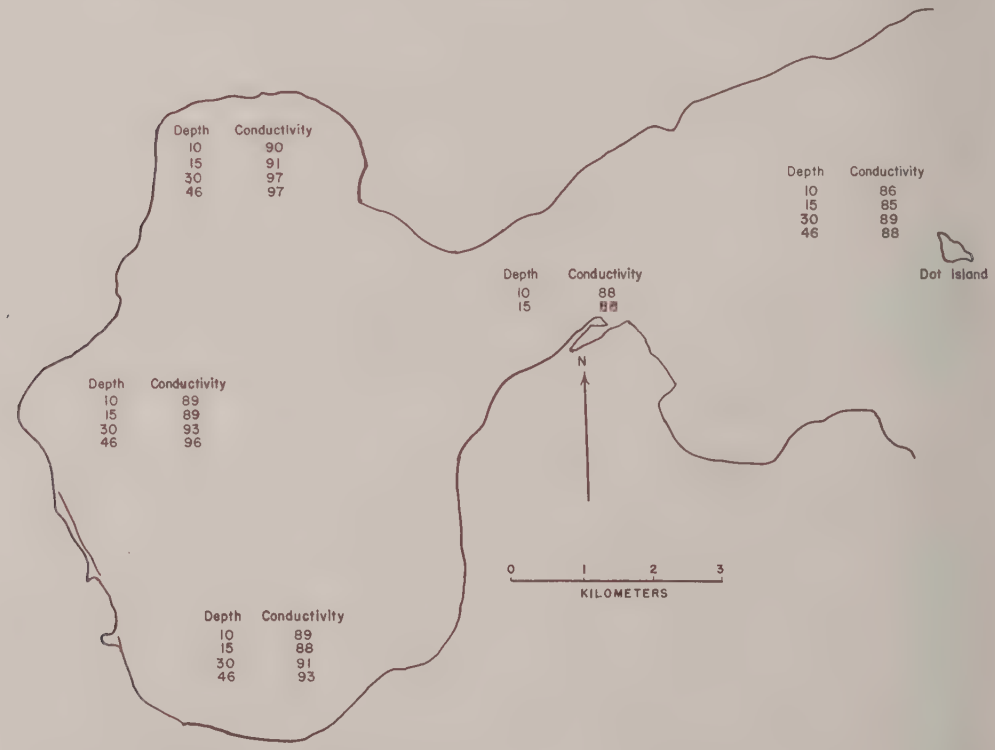


FIGURE 7.—Conductivities at different depths (meters) in West Thumb and near Dot Island on July 29, 1959.

Weather conditions in the summer of 1959 caused the water to stratify earlier than in 1957 or 1958 (fig. 5), which could presumably allow an oxygen deficit to increase. Measurements made on August 10, 1959, near Stevenson Island showed a deficit at 92 meters of 64 percent saturation. There is little question that during the short (approximately 45 days) period of complete stratification, a partial oxygen deficit develops below 30 meters in Yellowstone Lake. The relatively short period

of complete stratification, however, prevents a severe depletion that would influence the composition of bottom fauna or would even prevent fish from inhabiting this zone. Pennak (1955) found a greater progressive oxygen deficiency during the summer by depth in Bear Lake, Colo., than was present in Yellowstone Lake. His data on phytoplankton and carbon dioxide, however, suggested higher biological activity for Bear Lake.

Free carbon dioxide.—Free carbon dioxide existed in all samples collected during 1957. Readings ranged from 1.5 p.p.m. on the surface to 13.3 p.p.m., at 61 meters (table 8). The water depth, which showed a pronounced increase in carbon-dioxide content (above 10 p.p.m.), decreased from 45 meters in July to 19 in August. The depth of 19 m. in August was just below the metalimnion.

TABLE 8.—*Free carbon dioxide concentrations in mg./l., by month and depth during summer of 1957*

[Mean of readings at various stations]

Depth	June	July	August	September
0 meters	3.5	3.5		2.0
5 meters	3.8	4.3	3.5	3.4
10 meters	4.0	5.4	6.0	3.5
19 meters			12.5	4.0
30 meters		3.0		
45 meters		11.5	12.8	
61 meters			13.3	

BOTTOM TYPES

Types and distribution.—Bottom types in Yellowstone Lake consist of boulders, rubble, black obsidian sand, and fine clays with organic matter. Boulders are exposed in quantity only on the east shore and on the windward shore of Frank Island. Rubble areas are concentrated on the east shore and in a few exposed sections of the South and Southeast Arms. The most common shallow (less than 2 m.) water bottom type is black obsidian sand which contains less than one percent organic matter. Silty loams with varying amounts of organic matter make up more than 95 percent of the bottom type of Yellowstone Lake. The amount of organic matter in the bottom sediments increases with depth, with a correlation coefficient from 59 samples of 0.80 (table 9). In general, bottom soils below 50 m. possess more than 5 percent organic matter, while bottom soils between 25 and 50 meters have more than 2 percent organic matter. There are many exceptions to this condition which can be explained by water movements. Areas with a greater movement or exchange of water, such as the Southeast Arm with the inflowing Yellowstone River, allow a smaller amount of organic matter to accumulate than do other similar areas, such as the South Arm, with less water exchange. Water currents, as described earlier, prevented organic matter from accumulating in as great a quantity in the neck of West Thumb as in areas of similar depth inside West Thumb. Greater than average amounts of organic matter accumulated around Sand Point, where an eddy current is probably present, as shown from several drift recoveries. Organic matter deposition on the lake bottom of less than 20 meters in depth has much influence on fish distribution and fish food production. Those areas with much organic matter had large stands of aquatic plants, which had high standing crops of tendipedids and *Gammarus*. As shown later, the latter organisms are important foods for cutthroat trout.

Chemical properties.—Bottom-sediment samples were analyzed to determine what differences in organic carbon, nitrogen, P_2O_5, and cation exchange existed in sections of the lake by depth. Soil samples were all classified as silt loam in agricultural terminology and were typical of the

soft bottom sediments. The shallow stations had greater amounts of organic carbon and less phosphate (table 10) than the deeper stations. The cation exchange capacity was greater in the deeper stations. Nitrogen readings were not related to depth. The data show a greater utilization of nutrients in shallow water. With respect to growth conditions for aquatic plants, both Roelofs (1944) and Wohlschag (1950) found that organic matter content and site conditions were frequently of greater importance than phosphates, nitrates, or other nutrients, and these same factors appear to be most important in Yellowstone Lake.

TABLE 9.—*Percentage of organic matter in bottom soils by location and depth at 59 points in 13 sections of Yellowstone Lake*

Location and depth	Percentage of organic matter	Location and depth	Percentage of organic matter
West Thumb:		South end of Southeast Arm:	
25 meters	3.22	32 meters	4.64
52 meters	4.13	40 meters	3.20
70 meters	6.72	49 meters	3.58
71 meters	6.33	37 meters	2.08
75 meters	5.28	49 meters	1.94
85 meters	6.14	1 meter	0.89
88 meters	5.64	Mouth of South Arm:	
92 meters	5.81	88 meters	3.54
94 meters	6.38	53 meters	7.22
Neck of West Thumb:		58 meters	6.69
2 meters	0.31	South end of South Arm:	
13 meters	1.93	15 meters	9.12
37 meters	1.72	6 meters	6.40
Rock Point to Wolf Point:		1 meter	3.78
53 meters	1.75	Frank Island to Elk Point:	
22 meters	2.67	3 meters	0.22
70 meters	7.43	61 meters	5.85
64 meters	6.40	88 meters	5.42
Mouth of Flat:		88 meters	5.44
33 meters	6.40	79 meters	5.85
11 meters	1.48	Sand Point to Elk Point:	
Eagle Bay to Signal Point:		92 meters	6.71
6 meters	1.91	1 meter	3.66
63 meters	6.02	79 meters	8.33
12 meters	2.49	82 meters	5.90
67 meters	4.45	82 meters	6.00
75 meters	6.19	81 meters	6.24
75 meters	6.23	46 meters	4.68
Mouth of Southeast Arm:		Stevenson Island to Steamboat Point:	
40 meters	4.20	76 meters	6.43
69 meters	3.54	85 meters	6.31
76 meters	3.23	87 meters	6.88
49 meters	3.04	Stevenson Island to outlet:	
5 meters	1.22	31 meters	2.29
		55 meters	6.72
		53 meters	6.30

TABLE 10.—*Some chemical properties of six samples of bottom soils (silt loam) in Yellowstone Lake, collected August 15–30, 1958*

Location	Depth (meters)	pH	Organic carbon (percent)	Nitrogen (percent)	C/N ratio	P_2O_5 p.p.m.	Cation exchange capacity	Organic matter (percent)
Southeast Arm	40	6.5	2.60	.325	8.0	68	47.6	7.26
Southeast Arm	70	5.7		.262		118	58.0	
South Arm	15	6.8	3.70	.562	6.5	45	42.0	6.36
South Arm	3	6.0	3.38	.392	8.6	41	40.2	5.81
East of Stevenson Island	88	6.1	2.24	.415	5.3	280	54.0	3.85

AQUATIC PLANTS

The distribution and relative abundance of aquatic plants has a great bearing on the production of those bottom organisms which are important cutthroat trout foods. Collections of aquatic plants were made with a plant hook and while col-

lecting bottom samples with an Ekman dredge. The species collected and their depth distributions were as follows:

	Meters
Potamogeton richardsonii	1–5
Potamogeton praelongus	5–10
Potamogeton pusillus	1–18
Potamogeton robbinsii	5–10
Potamogeton gramineous var. *graminifolius*	0–3
Lemna trisulca	2–18
Ceratophyllum demersum	1–17
Najas flexilis	2–8
Myriophyllum exalbescens	1–5
Ranunculus aquaticus	0.5–5
Fontinalis sp.	2
Elodea canadensis	0–2
Nitella flexilis	1
Eleocharis sp.	0.5–1
Sagittaria cuneata	0.5
Sparganium sp.	0–2

Aquatic plant beds were generally restricted to protected littoral areas where organic matter was allowed to accumulate and were not present below a depth of 18 meters. The most extensive beds were located at 1 to 10 meter depths in South and Southeast Arms, on the lee sides of Stevenson and Frank Islands, and near the outlet. On windy, exposed shorelines, such as on the east shore or on the windward side of Stevenson Island, plant beds were dense from 7 to 15 meters. Aquatic plants in West Thumb were more abundant on the protected south shore than on the exposed north shore.

PLANKTON

Only general statements can be made about the abundance, seasonal changes, and genera of phytoplankton from samples collected in 1956. Plankton collections in 1957 and 1958 were aimed primarily at sampling zooplankters.

Phytoplankton.—The siliceous nature of the watershed undoubtedly caused the predominance of diatoms in the phytoplankton. Except for an annual August pulse of *Anabaena*, various diatoms such as *Asterionella*, *Melosira*, and *Stephanodiscus*, dominated the phytoplankton flora (table 11). A dense pulse of *Asterionella* occurred in 1955, 1956, 1957, and 1958, soon after the ice left in early June. This pulse extended to 35 m. in depth and was associated with high water levels due to melting snows. *Melosira* formed a pulse to a lesser extent in late July and remained abundant until September. *Anabaena* formed a heavy pulse during the first two weeks of August during all years measured. This pulse caused a green cast in

TABLE 11.—*Mean number of phytoplankton cells collected per liter (to nearest whole number) from all sections of Yellowstone Lake, June 28 to August 31, 1956*

[Each sample represents one plankton haul from 10 meters to surface]

Alga genus	Number collected during period—								
	June 28–July 6 (10 samples)	July 10–17 (14 samples)	July 20–24 (13 samples)	July 30–31 (5 samples)	Aug. 1–3 (7 samples)	Aug. 7–10 (11 samples)	Aug. 15–16 (5 samples)	Aug. 20–24 (8 samples)	Aug. 29–31 (3 samples)
Asterionella	128,711	115,896	24,764	54,955	2,349	961	1,566	583	1,073
Stephanodiscus	68	74	41	18	34	0	10	88	48
Melosira	2,138	903	61	0	260	132	2,125	43	128
Staurastrum	10	8	5	1	5	40	2	98	1
Coelastrum	0	14	14	0	12	4	1	20	82
Anabaena	889	123	591	7,420	16,807	11,830	17,998	389	0
Other [1]	1	11	11	1	3	2	4	33	6

[1] Includes *Coelosphaerium*, *Pleurococcus*, *Cosmarium*, *Naricula*, *Fragillaria*, *Ulothrix*, *Closterium*, *Pinnularie*, *Suriella*, *Compylodiscus*, unidentified desmids.

the water due to small clumps of algal filaments. Data from 1956 showed West Thumb to be the most productive section of the lake with Southeast Arm the least productive. Stations in the north and central areas of the lake were similar to those in South Arm and around Frank Island. These pulses were similar to those reported by Pennak (1955) for Grand Lake, Colo., although they were less intensive.

Zooplankton.—The zooplankton fauna consisted principally of *Conochilus unicornis*, *Diaptomus shoshone*, *Daphnia schoedleri*, and nauplii of *Diaptomus*. *Vorticella* occurred commonly during the *Anabaena* pulse in August, but no other species were commonly observed. A few *Cyclops* were identified, but they occurred so rarely (less than 0.1 percent) that they have been included with *Diaptomus* for purposes of enumeration. Also, a few *Diaptomus minutus* were identified. Forbes (1893) reported few *Cyclops*, but vast numbers of *Diaptomus*. *Keratella* was collected occasionally, but the rotifer fauna consisted almost entirely of *Conochilus unicornis*. Pennak (1957) found that one dominant species of copepod, cladoceran, or rotifer, was usually present in Colorado limnetic communities.

The vertical distributions of zooplankters showed that the depth range where the largest number occurred extended from 5 to 18 meters (table 12). *Diaptomus* were most abundant during July at 5 and 10 meters, but were present to 45 meters. Nauplii were most abundant during late July at the depth range of 15 to 23 meters. *Daphnia* were never abundant from any plankton samples, but increased in number in September. *Daphnia schoedleri*, the only cladoceran collected in Yellowstone Lake, is an inshore swarming species and was not sampled adequately at the

TABLE 12.—*Verical distribution of Diaptomus (Di), nauplii of Diaptomus (N), Daphnia (Da), and rotifers (R) during 1957 and 1958*

[Number per liter is derived from 10-liter samples combined from all limnological stations in Yellowstone Lake. Number of samples shown in parentheses. *Diaptomus* counts include a few *Cyclops*]

Depth and plankter	June 1–30	July 1–15	July 16–30	August 1–15	August 16–31	September 3–18	Mean number per sample
0 meters	(8)	(12)	(4)	(3)	(3)	(15)	(45)
Di	8.8	7.7	5.6	0.9	3.4	4.9	6.0
N	4.9	6.1	7.4	1.2	2.6	5.8	5.3
Da	0.2	0.1	0.1	0.3	0.1	2.3	0.9
R	0.2	0.5	37.2	0	5.5	2.4	4.6
5 meters	(7)	(11)	(8)	(11)	(12)	(16)	(65)
Di	10.5	18.7	21.7	13.7	13.2	14.9	15.4
N	8.7	11.8	10.2	10.9	12.0	13.8	11.6
Da	0.2	0.3	0.5	0.7	0.9	3.1	1.2
R	4.4	15.5	151.9	193.0	41.3	17.7	66.4
10 meters	(7)	(12)	(8)	(15)	(11)	(12)	(65)
Di	15.4	9.4	13.2	8.1	10.4	14.2	11.3
N	8.4	10.7	15.8	5.8	19.9	14.0	12.1
Da	0	0	0	1.7	0.8	3.5	1.2
R	1.2	17.2	85.0	61.5	51.2	22.5	40.8
15–18 meters		(5)	(3)	(15)	(8)	(9)	(40)
Di		3.2	5.1	3.4	5.0	11.7	5.7
N		7.7	46.9	15.2	16.2	18.1	17.5
Da		0	0.4	0.1	0.7	1.1	0.5
R		0.3	168.0	53.2	59.1	10.6	46.8
21–23 meters			(1)	(6)	(1)	(2)	(10)
Di			3.5	2.1	2.7	8.9	3.7
N			55.7	8.0	17.7	15.0	15.1
Da			0	0	0	2.1	0.2
R			2.3	1.4	4.2	24.3	6.3
30 meters		(2)	(2)	(6)		(5)	(15)
Di		10.5	4.3	1.2		4.2	3.9
N		11.0	17.4	2.1		9.1	7.7
Da		0	0	0.1		0.6	0.2
R		3.5	2.2	2.7		2.0	2.5
45 meters		(1)		(1)	(1)		(3)
Di		8.0		1.2	2.4		3.9
N		6.7		4.1	0.7		3.8
Da		0		0	0		0
R		0		0.6	0		0.2

various stations for this reason. In late August, 1959, two large swarms covering an estimated 14,000 cubic meters each were observed, and each swarm contained 400 to 500 *Daphnia* per liter. These concentrations were located by anglers who were taking advantage of the fish concentrations in these areas. The intensity of these swarms probably varies annually, since such large concentrations would probably have been observed previously. Tonolli (1954) found that annual cladoceran populations varied greatly in Italian alpine lakes due to meteorological conditions. He found that warmer weather increased populations significantly, and related these conditions to the velocity of cladoceran developmental processes. The concentration in 1959 may have been due to the fact that the epilimnion formed earlier than in other years observed (fig. 5). Rotifers were abundant from the middle of July to mid-August, and they extended in abundance down to 18 meters. Those plankton organisms important as food for cutthroat trout did not extend in abundance below 18 meters in depth.

The abundance of zooplankters amongst different sampling stations can be compared from our data on table 13. The Southeast Arm (Station J) showed the lowest numbers. This fact is probably due to the great exchange of water from the inflowing Yellowstone River and to the low amount of nutrients in this arm. *Diaptomus* and nauplii were never abundant in this section of the lake. The West Thumb section showed poor standing crops and this was due to the continual removal of surface water from this area as shown both by current and temperature information. The heaviest populations were in the northeast and central parts of the lake where surface water accumulates from wind action. McMahon (1954) found that the movement of surface water due to wind action also concentrated entomostracan plankters in the lee sections of Lakelse Lake, British Columbia, Canada. The extreme north section of the lake and the South Arm were similar in numbers collected. The large number at Station F on the lee side of Frank Island is believed to be due to its protected nature.

TABLE 13.—*Mean number of organisms per liter from June 15 to September 15, 1957, among 10 sampling stations in Yellowstone Lake*

[All samples collected at 5- and 10-meter depths and separated as *Diaptomus* (Di), nauplii of *Diaptomus* (N), *Daphnia* (Da), and rotifers (R). Sampling stations shown in figure 1]

Month and station	Number of samples	Di	N	Da	R
June:					
A	2	1.4	1.2	0	0
B	2	3.0	0.7	0	0
C					
D					
E	2	22.1	15.0	0	9.4
F	2	32.0	20.1	0.2	.0
G					
H	2	11.7	11.4	0	0
I	2	20.0	14.4	0.5	0
J	2	0.3	0	0	0
July:					
A	4	16.3	10.2	0.2	39.1
B	2	22.5	13.3	0	7.0
C	2	21.2	21.6	0	353.6
D	2	21.6	14.3	0	10.1
E	2	20.5	34.3	0	57.7
F	3	19.5	6.3	0	253.0
G	2	12.9	10.8	0	71.4
H	4	22.5	12.8	0	42.1
I	4	18.8	17.4	0.7	53.0
J	4	8.7	4.4	1.2	55.5
August:					
A	4	13.0	8.8	0.8	119.4
B	4	25.7	15.3	1.6	84.1
C	4	13.7	15.3	5.8	61.8
D	4	13.4	14.7	0.1	166.2
E	3	13.7	12.7	0.7	80.5
F	4	15.8	13.7	1.1	170.8
G	2	10.4	6.6	0.9	36.5
H	4	11.4	24.4	0	117.1
I	4	8.8	14.8	0.5	36.6
J	4	4.6	9.4	2.1	50.9
September.					
A	2	6.1	8.5	1.4	39.3
B	1	3.2	6.8	0	22.8
C	1	15.1	8.0	3.7	0
D	2	5.6	3.7	0.9	9.3
E					
F	2	8.2	13.4	1.8	24.4
G	2	10.9	3.2	2.0	6.2
H	2	7.3	16.1	0.9	8.4
I	1	17.9	21.3	1.1	11.2
J	1	5.2	10.4	6.5	9.1

	Di	N	Da	R	All organisms
Mean, all samples:					
A	11.0	8.0	0.6	59.4	79.0
B	17.4	10.7	0.7	41.5	70.3
C	16.0	16.1	3.8	136.3	172.2
D	13.5	11.8	0.3	88.0	113.6
E	18.0	19.5	0.3	53.7	91.5
F	18.4	12.8	0.8	135.5	167.5
G	11.4	6.9	0.9	38.0	57.2
H	14.5	17.0	0.2	54.4	86.1
I	15.3	16.3	0.6	33.6	65.8
J	5.4	6.0	1.8	39.5	52.7

BENTHOS

Studies on benthos included the determination of vertical and horizontal distribution of the common organisms. The sampling of hard-botton areas of the littoral zone was sparse, but observation did not disclose any great concentrations of organisms in these areas, possibly because of heavy molar action. Undoubtedly, the numbers of Ephemeroptera and Trichoptera were much higher than our sampling disclosed. The common organisms present, their depth distribution, and abundance were as follows:

Lumbriculidae (usually *Limnodrilus* sp.)—sparsely present 0 to 95 meters on silty bottom.

Tubifex tubifex (O. F. Muller)—only occurred in abundance in clumps on delta of Yellowstone River in Southeast Arm—10 meters.

Helobdella stagnalis (Linnaeus)—sparsely distributed in entire lake down to 15 meters on silt bottom.

Hyallela azteca (Saussure)—common from 0 to 15 meters around aquatic plant bed.

Gammarus lacustris (Sars)—abundant on protected shores down to 30 meters—present to 43 meters—most abundant around aquatic plant beds.

Ephemerella sp.—common only on poorly sampled, rocky shorelines, from 0 to 8 meters.

Psychomyia sp.—rare from 1 to 5 meters.

Dicosmoecus sp.—common from 0 to 25 meters.

Tendipes (*Tendipes*)—abundant from 0 to 30 meters.

Tendipes (*Limnochironomus*) — moderately abundant to 90 meters.

Prodiamesa—present at all depths and most abundant from 70 to 90 meters.

Procladius—moderately abundant to 30 meters.

Pisidium—present from 0 to 30 meters.

Sphaerium—present from 20 to 60 meters.

The standing crops of benthic organisms at various depth ranges showed that the 6- to 11-meter range was the most productive in number, with a mean of 1,036 organisms per square meter (table 14). This large production was composed principally of Oligochaetes (*Tubifex*), *Gammarus*, and *Hyallela*. *Gammarus* extended in moderate abundance to 23 meters, but the largest concentration was in the 1- to 5-meter range. Tendipedids were most abundant in the 6- to 11-meter range, but were numerous down to 92 meters. Sphaeriids were common at 1- to 5-meters. The highest numbers of *Gammarus* were found around aquatic plant beds of *Potamogeton pusillus* and *Lemna trisulca*, but fish predation (to be discussed later) undoubtedly influenced these numbers.

TABLE 14.—*Mean number of bottom organisms collected per square meter at various depth ranges in Yellowstone Lake, June 15 to September 18, 1957, and July 15 to August 30, 1958*

[N=number collected; F=frequency of occurrence]

Organism	Collected at depths of—											
	0–5 meters (16 samples)		6–11 meters (32 samples)		12–17 meters (30 samples)		18–23 meters (11 samples)		24–58 meters (21 samples)		61–92 meters (5 samples)	
	N	F	N	F	N	F	N	F	N	F	N	F
Oligocheata	5	4	366	14	23	15	36	7	42	14	39	3
Hirudinea	20	6	70	21	7	6	0	0	13	3	4	1
Sphaeriidae	22	7	4	3	4	5	4	1	4	2	0	0
Tendipedidae	34	8	83	20	295	25	245	10	497	21	280	3
Gammarus lacustris	537	15	295	28	158	21	178	6	54	9	0	0
Hyallela azteca	153	8	216	14	84	6	3	1	0	0	0	0
Trichoptera	11	4	2	2	0	0	0	0	0	0	0	0
Ephemeroptera	2	2	0	0	0	0	0	0	0	0	0	0
Hydracarina	3	1	0	0	0	0	0	0	0	0	0	0
Gastropoda	1	1	0	0	1	2	0	0	0	0	0	0
Total	788		1,036		572		466		610		323	

The number of organisms per square meter is low when compared with those found in similar studies. Reimers, Maciolek, and Pister (1955) reported more organisms per unit area for their lakes in the Sierras, although only Lake Mildred contained many amphipods. The number per square meter also was lower down to 60 meters than Rawson (1953) reported for Great Slave Lake. The latter author also compared the percentage composition of the dominant kinds of bottom organisms from several large North American lakes; the Yellowstone Lake bottom fauna was similar, except that *Gammarus* replaced *Pontoporeia* as the dominant amphipod. Calhoun (1944a) found a higher standing crop in Blue Lake, Calif., than in Yellowstone, but found a rapid drop in production below 20 meters.

The number of bottom organisms in different areas of Yellowstone Lake was compared from 2 to 15 meters (table 15). The largest numbers were collected off Lake Area in the northern area of the lake. The lowest number was off Clear Creek, which is an exposed wave-swept shoreline where organic matter does not accumulate. A lower number than would be expected was present in the South Arm and near Frank Island. Most of the differences between these latter two stations and lake were in numbers of *Gammarus*, which is an important food for cutthroat trout. The low production in Southeast Arm was possibly due to a large accumulation of fine silt and to the shifting bottom.

TABLE 15.—*Number of bottom organisms per square meter at six stations in Yellowstone Lake in 1958*
[Samples ranged in depth from 2 to 15 meters at about 3-meter intervals]

Organism	West Thumb off Solution Creek, August 5; bottom sand with little silt (6 samples)	Southeast Arm off Trail Creek, July 31; bottom fine silt with little sand (6 samples)	South Arm near Peale Island, August 12; bottom sand, gravel, and silt (6 samples)	Off Clear Creek, July 25; bottom sand, gravel, little silt (4 samples)	North side of Frank Island, August 7; bottom sand, gravel, and silt (5 samples)	Lake Area, July 28 and August 15; bottom sand, gravel, and silt (6 samples)
Oligochaeta	0	2	20	0	4	24
Hirudinea	0	0	32	11	32	48
Hyallela azteca	203	34	54	30	176	602
Gammarus lacustris	317	99	206	99	435	919
Hydracarina	7	0	0	0	0	11
Ephemeroptera	4	0	0	0	0	3
Trichoptera	11	2	0	0	0	0
Tendipedidae	39	66	63	27	54	108
Gastropoda	0	2	0	0	0	0
Sphaeriidae	4	11	18	0	15	18
Total	585	216	393	169	716	1,733
Mean number per sample	99.5	36.0	65.5	42.3	143.2	288.8

VERTICAL DISTRIBUTION OF CUTTHROAT TROUT

During the open-water season, cutthroat trout in Yellowstone Lake rarely venture below 20-meter depths. During 1957 and 1958 more than 99 percent of the cutthroat trout were captured in the upper 25 meters of water, in 92 gill-net sets (table 16). Of the total, 63 percent were collected from the surface to 15 meters, and no trout were captured below 30 meters. This type of vertical distribution of cutthroat trout has been documented by McConnell, Clark, and Sigler (1957) for Bear Lake in Utah and Idaho, although the cutthroat population was small.

Our data do not conclusively show great variations in vertical distribution among different size groups, but small trout (155–200 mm., predominently age group II) frequented water below 20 meters more than did larger trout.

TABLE 16.—*Number of cutthroat by size groups captured by 92 overnight experimental gill-net sets at different depth ranges in Yellowstone Lake during July and August of 1957 and 1958*

Depth	Number of sets	Number in size group range—								Total
		Less than 100 mm.	105–150 mm.	155–200 mm.	205–250 mm.	255–300 mm.	305–350 mm.	355–400 mm.	Above 400 mm.	
0–5 meters	11	0	0	25	30	45	55	60	4	219
6–9 meters	11	0	0	51	30	36	57	39	1	214
10–15 meters	22	0	0	40	16	21	38	43	2	160
17–20 meters	11	0	0	6	3	3	25	28	0	65
21–25 meters	22	1	0	23	3	0	10	9	0	46
26–30 meters	8	0	0	1	2	1	1	1	0	6
31–46 meters	7	0	0	0	0	0	0	0	0	0
Total	92	1	0	146	84	106	186	180	7	710

FOOD OF CUTTHROAT TROUT

The most abundant organisms found in the stomachs of cutthroat trout in Yellowstone Lake were *Daphnia shoedleri*, *Gammarus lacustris*, and various species of Tendipedidae (table 17). *Diaptomus shoshone*, Trichoptera, Plecoptera, and Ephemeroptera occurred in fewer stomachs. The seasonal changes in feeding habits showed that *Gammarus* was most important in mid-July, but declined in importance in August. The number of *Daphnia* increased from July to October and is believed due to the swarming habit during the latter part of the summer. Tendipedidae pupae and adults were common in stomachs during July or when the major emergences occurred. Tendipedidae larvae were not utilized heavily. *Diaptomus* occurred in few stomachs in July, but assumed greater importance later in the season. Only three stomachs out of 409 contained fish, and these were cutthroat trout.

Feeding habits of trout by size groups showed that both *Gammarus lacustris* and *Daphnia schoedleri* were the most commonly utilized foods of all sizes of trout (table 18). There was a gradual transition in the range of 275 to 325 mm. from a zooplankton-bottom fauna diet to a predominantly bottom fauna diet. *Diaptomus* were rarely utilized above 250 mm., and *Ephemerella* nymphs and Trichoptera were most important among large fish. From our knowledge of the distribution of the food organisms in the lake, it appears that small trout feed both in the limnetic and littoral zones while large trout feed almost entirely in the littoral zone. *Daphnia schoedleri*, the only zooplankter found in many stomachs of large trout, is an inshore swarming species.

Differences in feeding habits in two sections of Yellowstone Lake were demonstrated from the stomach contents of 344 cutthroat trout caught at Fishing Bridge and West Thumb docks (table 19). Stomachs from fish caught at Fishing Bridge contained many stream organisms and some trout eggs. Trout from West Thumb utilized terrestrial organisms more so than trout from Fishing Bridge. Many stomachs from Fishing Bridge contained both *Diaptomus* or *Daphnia* and stream bottom insects, which indicates that cutthroat trout can rapidly change their feeding

habits to utilize a different type of food. The large number of terrestrial insects from West Thumb included the wind-blown bark beetles, wasps, and others, which were carried into the water by the predominant south and southwesterly winds from the lodgepole-pine forests.

Calhoun (1944b) found that cutthroat trout (*Salmo clarkii henshawi*) utilized *Tendipes* larvae more commonly than

TABLE 17.—*Stomach contents of 409 cutthroat trout captured by gill nets, by time of capture in 1958*

[All sizes combined. P=percent of stomachs containing organisms; M=mean number, to nearest 1.0, of food organisms per stomach. Collected from South Arm, Lake Area, West Thumb, and Southeast Arm]

Food organism	July 15–31 (238 fish)		August 1–15 (100 fish)		August 16–31 (43 fish)		October 15 (28 fish)	
	P	M	P	M	P	M	P	M
Daphnia	19.7	209	24.0	295	37.2	72	82.1	976
Diaptomus	2.1	223	3.0	541	7.0	158	14.2	93
Gammarus lacustris	56.7	25	41.0	27	30.2	9	17.8	105
Hyallela azteca	1.3	5	1.0	15	2.3	65	0	0
Hydracarina	2.5	5	0	0	0	0	0	0
Plecoptera	1.3	1	2.0	2	4.7	1	0	0
Ephemerella	10.1	13	3.0	3	0	0	0	0
Trichoptera	6.3	13	8.0	4	0	0	0	0
Tendipes larva	8.8	19	4.0	2	0	0	0	0
Tendipes pupa	23.5	20	10.0	11	4.7	2	0	0
Tendipes adult	20.6	28	8.0	4	2.3	1	0	0
Prodiamesa	0.4	1	0	0	0	0	0	0
Procladius	1.3	4	0	0	0	0	0	0
Hymenoptera and Coleoptera	1.7	8	1.0	2	0	0	7.1	13
Gastropoda	2.1	5	0	0	0	0	0	0
Pisidium	0.8	3	0	0	0	0	0	0
Trout eggs	0.4	4	0	0	0	0	0	0
Trout	0.4	1	0	0	2.3	4	3.6	1
Number of stomachs empty	30		16		11		0	

TABLE 18.—*Stomach contents of 298 cutthroat trout captured by gill nets during July and August 1958, by length groups*

[P=percent of stomachs containing organisms; M=mean number of organisms per stomach, to nearest 1.0]

Food organisms	Trout size range													
	150–200 (41 fish)		205–250 (66 fish)		255–275 (30 fish)		280–300 (19 fish)		305–325 (37 fish)		330–350 (45 fish)		355–400 (60 fish)	
	P	M	P	M	P	M	P	M	P	M	P	M	P	M
Daphnia	43.9	381	42.4	477	33.3	349	52.6	749	24.3	343	24.4	267	25.0	189
Diaptomus	12.2	215	7.6	273	0	0	0	0	0	0	2.2	200	1.7	80
Gammarus	36.6	13	39.4	24	36.7	11	57.9	32	40.5	24	44.4	26	51.7	30
Hyallela	7.3	6	0	0	0	0	0	0	2.7	15	2.2	65	0	0
Hydracarina	0	0	3.0	10	0	0	5.3	1	5.4	4	0	0	3.3	3
Plecoptera	2.4	1	1.5	1	0	0	0	0	2.7	1	0	0	0	0
Ephemerella	9.8	2	10.6	2	6.6	16	5.3	2	2.7	1	4.4	33	3.3	48
Trichoptera	0	0	4.5	2	1	75	5.3	1	13.5	7	4.4	5	1.7	24
Tendipes larva	4.9	3	4.5	15	3.3	49	5.3	3	0	0	2.2	3	6.7	25
Tendipes pupa	17.1	14	9.0	15	16.6	26	21.0	5	8.1	15	24.4	17	20.0	32
Tendipes adult	7.3	24	10.6	17	20.0	42	0	0	5.4	29.	15.6	5	8.3	54
Prodiamesa	2.4	125	0	0	0	0	0	0	0	0	0	0	0	0
Procladius	0	0	0	0	0	0	5.3	3	0	0	2.2	8	1.7	2
Hymenoptera and Coleoptera	0	0	1.5	2	3.3	20	0	0	5.4	5	2.2	2	1.7	2
Gastropoda	0	0	1.5	7	0	0	0	0	0	0	2.2	7	1.7	2
Pisidium	0	0	0	0	0	0	0	0	0	0	0	0	3.3	3
Trout	0	0	0	0	0	0	0	0	2.7	1	0	0	1.7	1
Number of stomachs empty	8		5		4		2		8		6		17	

pupae in Blue Lake, due to a scarcity of other food organisms. He also found that plankton crustacea were used more commonly than *Gammarus* and immature chironomids in a more productive lake. Some workers have mentioned the piscivorous nature of cutthroat trout (Echo, 1956; McConnell, et al., 1957) when large populations of forage fishes are present. Irving (1956) found mostly *Gammarus* and *Tendipes*, but few fish, in cutthroat trout from Henrys Lake, in spite of the large number of forage species available. In general, cutthroat trout food studies have shown a preference for macrozooplankters and bottom organisms over fish, except where unusually large cutthroat occur.

TABLE 19.—*Stomach contents of 344 cutthroat trout caught by angling in the vicinity of Fishing Bridge and West Thumb docks from June 5 to August 15 in 1957 and 1958*

[P=percent of stomachs containing organisms; M=mean number of organisms per stomach, to nearest 1.0]

Food organism	Fishing Bridge (169 fish)		West Thumb (175 fish)	
	P	M	P	M
Gordius	2.4	4	0	0
Daphnia	11.2	171	8.6	128
Diaptomus	10.7	1,213	16.6	714
Gammarus lacustris	18.9	12	33.7	21
Hyallela azteca	0.6	145	0	0
Plecoptera	8.9	7	2.3	3
Ephemeroptera	14.2	14	12.0	34
Odonata	0	0	0.6	1
Hemiptera	0	0	1.1	3
Trichoptera	10.7	6	3.4	8
Hymenoptera and Coleoptera	4.1	8	16.0	10
Tendipes larva	6.5	7	4.6	6
Tendipes pupa	20.7	30	37.7	22
Tendipes adult	5.9	10	22.9	31
Procladius	1.8	16	0	0
Pisidium	1.8	2	0	0
Cutthroat trout and eggs	11.2	8	0	0
Number of stomachs empty	38		15	

TROUT DENSITY AND LIMNOLOGY

Angling pressure on Yellowstone Lake is concentrated in the northern area and, to a lesser extent, in West Thumb, owing to the lack of access in the southern sections. The total catch by area from 1950 to 1959 showed that an average of 66.7 percent of the fish were removed from the northern area, an average of 24.8 percent from West Thumb, and an average of 8.5 percent from the southern area (table 20). The northern area occupies 25.4 percent of the lake area, West Thumb 19.1 percent, and the southern area 55.5 percent.

Three possible effects of this unequal harvesting of trout in the northern area were (1) fewer trout in relation to food abundance, (2) large numbers of bottom organisms owing to lack of predation, and (3) movements of trout into the area.

First, gill-netting in different sections of the lake showed fewer trout off Lake Area than would be expected from the habitat and the large amount of food (table 21). All gill-netting was carried out after the major spawning runs had stopped. The largest number were caught in the South Arm and around Frank Island. The scarcity of trout off Clear Creek was due to the exposed wind-swept nature of the shoreline. The scarcity of trout in Southeast Arm is believed to be due to the low food production and the fact that gill-netting was on the delta of the Yellowstone River, which cutthroat do not frequent because of the shifting bottom.

TABLE 20.—*Percentage of trout caught in each of three areas of Yellowstone Lake, by years, 1950 to 1959*

Year	Percent caught in—			Number caught
	Northern area	West Thumb area	Southern area	
1950	69.4	24.6	6.0	200,015
1951	69.3	24.3	6.4	208,255
1952	68.7	23.4	7.9	245,277
1953	66.6	23.7	9.6	195,873
1954	69.1	22.0	8.9	215,933
1955	66.9	25.1	8.0	286,056
1956	64.0	25.6	10.4	290,221
1957	63.4	26.9	9.7	301,155
1958	64.7	25.3	10.0	349,027
1959	64.6	27.1	8.3	393,467
Mean	66.7	24.8	8.5	

TABLE 21.—*Number of trout of more than 200 millimeters, total length, captured in depths of 0 to 20 meters in six areas of Yellowstone Lake by 38 overnight experimental gill-net sets in 1958*

Sampling area	Date of set	Number of sets	Number of trout caught	Mean catch per set
Lake	July 25–Aug. 18.	6	66	11.0
Middle South Arm	Aug. 13	3	47	15.6
Peale Island	July 15–24	14	219	15.6
Southeast Arm	July 31	3	29	9.6
Clear Creek	Aug. 19	3	20	6.6
Frank Island and Plover Point.	Aug. 8–13	9	125	13.9

Second, bottom organisms in the northern area were more numerous than would normally be expected from the bottom types or abundance of aquatic plants (table 15). The number of organisms above 15 meters at Lake Area averaged 288.8, whereas the nearest recorded number in other sections of the lake was 143.2 at Frank Island. The greater abundance of bottom organisms in the northern area was due to more *Gammarus* and *Hyallela*, the principal foods of the cutthroat trout. The most plausible reason for the large number of bottom organisms at Lake Area is the lack of trout predation on bottom organisms due to rapid recruitment by angling. Both Ball and Hayne (1952) and Reimers (1958) demonstrated that fish populations can severely deplete bottom fauna populations. Wohlschlag (1950) found that bluegills fed more heavily in areas of heavy chironomid production than in areas of low production.

Third, trout apparently moved into the northern area. This movement was believed to be for feeding or to take advantage of the high standing crop of bottom food, since most movement occurred after the spawning period. From 1949 to 1955, 18,836 trout were tagged in five spawning streams, and the returned tags that included sufficient information on catch location were used to compare the general movements of postspawning trout from five spawning streams (table 22), (Ball and Cope 1961). The data on fish movement can be summarized as follows: Those fish tagged in Pelican Creek were usually recovered in the northern area and around Fishing Bridge. Clear Creek fish also were captured in the northern area, particularly in Bridge Bay. Fish tagged in Chipmunk and Grouse Creeks, at the lower end of South Arm, were most commonly captured in the southern area or in West Thumb, although 25 percent were captured in the northern area. There was a movement of postspawners from Chipmunk and Grouse into West Thumb and, to a lesser extent, into the northern area in August, and many were captured in these locations during the year following tagging. From the movements of postspawners, the only evidence of a long-distance movement from the spawning stream to the area of capture was the large number of fish tagged in South Arm that moved into West Thumb and into the northern area. A lesser movement was apparent from those fish tagged in Arnica Creek and recovered on the west shore of the northern area of the lake. In general the postspawners recovered the second year after tagging dispersed more than those caught the first year.

TABLE 22.—*Movements of cutthroat trout after spawning, as determined from fish tagged in five spawning streams and recaptured by angling, 1949–55*

Spawning stream	Number of fish tagged	Number of tag returns	Percent of all returns captured in—		
			Northern area [1]	Southern area	West Thumb area
Arnica Creek	4,948	271	26.2	4.4	69.3
Pelican Creek	6,043	422	88.9	4.5	6.6
Clear Creek	1,100	54	70.3	12.9	16.7
Chipmunk and Grouse Creeks	6,745	160	25.0	41.9	33.1
Total	18,836	907			

[1] Includes 18 returns from Yellowstone River.

Heavy fishing pressure undoubtedly influenced the number of tag returns from the northern area. The estimated annual

fishing pressures, in hours per acre, from 1950 to 1954 were northern 10.5, West Thumb 4.9, and southern 0.6. The fishing mortality rates (percent) for postspawning trout from five spawning streams were as follows: Pelican, 12.2; Arnica, 9.3; Chipmunk, 5.2; Grouse, 3.7; and Clear, 9.4 (Ball and Cope 1961). These fishing mortality rates show that fish from Pelican, Arnica, and Clear Creeks are subjected to a greater fishing pressure than fish from Chipmunk and Grouse, but the ratios are not so different as the fishing pressure per acre for the three areas of the lake; thus, there must have been a greater movement of trout into the northern area or to West Thumb than away from it.

From the location of tag recoveries, there appeared to be a tendency for postspawning trout to follow the shoreline of greater standing crops of food organisms from their spawning streams to their point of capture, although such was not always true. It was particularly true, however, for fish from Chipmunk, Grouse, and Arnica Creek. These data support the hypothesis that feeding may be an important factor in causing trout to move out after spawning.

There was a greater concentration of planktonic entomostraca in the northeast part of the lake due to surface currents, but the food of postspawning trout is principally bottom organisms, and a large standing crop of bottom foods would be more important than plankton in causing any fish to migrate.

BIOLOGY OF YELLOWSTONE LAKE

Yellowstone Lake has many characteristics of the large oligotrophic lakes of Canada or of the northern Great Lakes, but its bottom fauna and fish compositions are notably different. The other lakes have *Pontoporeia* or *Mysis* as the dominant bottom fish-food organism, and all have large populations of coregonids. Undoubtedly, factors which have prevented introduction of these organisms into Yellowstone Lake include the impassable falls 15 miles below the lake outlet and the altitude.

An interesting comparison between the mean depths of the large lakes of Canada and the northern Great Lakes and the annual commercial fish production (lbs. per acre) has been prepared by Rawson (1955). He constructed a curve and found that fish production decreased with increasing depth on a relatively smooth curve. A comparison of the mean depth of Yellowstone Lake (139 ft.) and its mean sport-fish production from 1950 to 1959 (2.15 lbs. per acre) shows that it fits into this curve closely between Lake Nipigon (1.07 lbs. per acre, and mean depth 180 ft.) and Lake Winnipeg (2.66 lbs. per acre, and mean depth 43 ft.). It is surprising that the sport-fishery production of Yellowstone Lake with only one fish species fits so well into this curve when the commercial fish production of these lakes involves many fish species and several fish predator-and-prey relations.

The limnological classification of Yellowstone Lake according to Lundbeck (1934) would be primary oligotrophic, since it is poor in nutrients and has low temperatures. The volcanic nature of the drainage, with deficiencies in calcium and other minerals, probably has as great an influence in limiting production as has morphometry. Turbidity and too great a water exchange are not limiting factors in Yellowstone as mentioned for Port John Lake, British Columbia (Robertson, 1954), which has a similar water chemistry but a high rate of water replacement. The low number of plankters per liter in

Yellowstone Lake is partly offset by the depth of its trophogenic zone. Ohle (1956) stated that deep lakes may have a lower production density, but this deficiency is compensated for by a greater production depth than shallow lakes. The great production depth of Yellowstone Lake is shown from the depth distribution of aquatic plants, bottom fauna, and plankton. Secchi disk records, which reflect plankton density, showed high readings.

The development and use of Yellowstone Lake is controlled by the National Park Service. This control has prevented artificial eutrophication as has occurred in several large oligotrophic lakes (Edmundson et al., 1956). The data collected by Forbes (1893) in 1890 were not quantitative, but a comparison of his observations with the data in this report indicates that the dominant species composition of zooplankters, phytoplankters, and bottom organisms did not change from 1890 to 1957.

Few large lakes have as few fish species as Yellowstone, but it appears that the cutthroat are utilizing the available animal food rather efficiently. The depth range of the trout is closely related to the depth distribution of both the predominant bottom foods and planktonic foods. The kinds of food utilized by different sizes of trout overlap to a great degree, although there is a gradual transition from a bottom fauna–zooplankton diet to a predominantly bottom-fauna diet in the range of 275 to 325 mm. (table 18). This change in feeding habits occurs in the same length range when trout first become available to the sport fishery in numbers. A length frequency curve of the catch for 1959 shows that the slope begins to increase around 275 mm., but that the greatest increase takes place above 315 mm. (fig. 8). The reason the catch does not include more small trout (below 12 inches) is not that they are caught and returned to the lake,

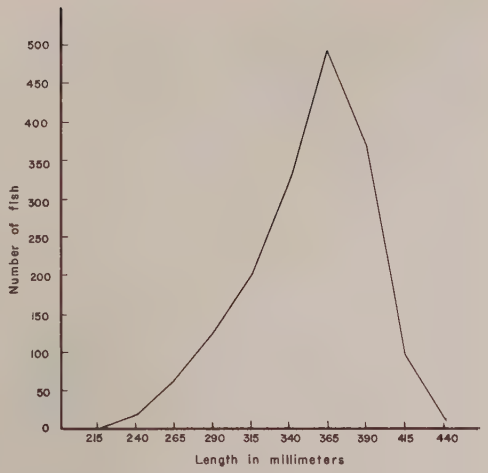


FIGURE 8.—Length frequency of anglers' catch from Yellowstone Lake in 1959 from sample of 1,690 fish. Points represent medians of 25-mm. groups.

since many anglers will keep trout around 10 inches. These trout are difficult to catch [1] and are dispersed more in the lake owing to their feeding habits. Small trout feed both in the limnetic and littoral zone, while large trout feed in the littoral zone. The greater dispersal of small trout makes them less vulnerable to angling. Another probable effect of this great dispersal is the low rate of predation on small trout by large trout as shown by food studies. This fact also accounts for the high survival rate of 36 percent which Ball and Cope (1961) suggest exists from the time that immature fish leave the parent stream until they return as spawners.

The only competitive species appears to be the longnose sucker, since recent studies (unpublished) have shown that suckers feed primarily on the same bottom organisms as the cutthroat trout. Past data on

[1] Madsen in an unpublished report (Age and growth of the cutthroat trout (*Salmo lewisi*) in Yellowstone Lake, Wyoming, dated May 15, 1940) attempted to determine why anglers rarely caught small trout and found that small trout would rarely take any lure, even when schools were located.

the sucker population in Yellowstone Lake are lacking, although records from the Yellowstone Fish Cultural Station indicate that the sucker was introduced in 1923 or 1924. Numbers of suckers recorded in the spawning runs in Pelican Creek showed a general increase up to 1950 and a leveling off since that year. The competition with the cutthroat trout appears to be increasing, although there has been no clear evidence of detrimental influence on the trout population.

SUMMARY

Limnological studies on Yellowstone Lake, Yellowstone National Park, were conducted from 1954 to 1959. Geological evidence indicates that the original basin was formed from a subsidence or readjustment of the laval flows in the Eocene. Hot springs still exist in the drainage basin and in the lake. Annual water-level fluctuation is less than 1.8 meters. The lake lies at an altitude of 2,358 meters and has the following dimensions: Surface area, 35,391 hectares; mean depth, 42 meters; basin capacity, 14 x 10^9 cubic meters; maximum depth, 95 meters; and shoreline development, 3.04. A contour map is included.

Water-current studies showed a large surface-water movement from the south and southwest to the north and northeast parts of the lake. Compensatory subsurface currents were found by bottom-current studies. Water-temperature data showed various stages of stratification from late May and early June when the ice left until late July when complete stratification was evident. Differences in water stratification between West Thumb and the northeast part of the lake were related to surface-water movement. High water levels in certain years were associated with deep epilimnion layers.

Water composition showed HCO_3 to be the major anion and Na to be the major cation. Conductivities were highest in West Thumb and lowest in Southeast Arm. Upwelling is believed to have caused the high readings in West Thumb. Protected stations had lower conductivities than exposed stations, and the causative factor was believed to be the thinner epilimnion strata in the protected stations which caused a more rapid utilization of nutrients by plankton. Oxygen concentrations were usually above or near saturation, although deficits developed in the hypolimnion during 1957 and 1959. Free carbon dioxide was present in all samples and concentrations above 10 p.p.m. were found below the metalimnion.

Bottom types included boulders, rubble, black obsidian sand, and fine clays with organic matter. Amount of organic matter in the soft sediments increased with depth, but lake areas with strong currents had low amounts of organic matter. Greatest concentrations of soil nutrients were in deep water. A list of aquatic plants and their depth ranges is presented. The depth limit of all higher aquatic plants was 18 meters.

The diatoms *Asterionella*, *Melosira*, and *Stephanodisus* were abundant. A dense pulse of *Anabaena* was observed in August. Principal zooplankters were *Conochilus unicornis*, *Diaptomus shoshone*, and *Daphnia shoedleri;* largest concentrations ranged from 5 to 18 meters. Several large swarms of *Daphnia shoedelri*, an inshore swarming species, were observed in 1959. Benthos consisted principally of *Gammarus lacustris*, *Hyallela azteca*, oligochaetes, and tendipedids. Ex-

cept for tendipedids, which were present at all depths, bottom organisms were rare below 23 meters.

Cutthroat trout were concentrated in the upper 15 meters of water and were rare below 25 meters. Most abundant food organisms in trout stomachs in the summer season were *Gammarus lacustris*, *Daphnia shoedleri*, and tendipedids. *Gammarus* were important in June and July, and *Daphnia* in August and September. Small trout utilized both bottom organisms and zooplankton, while large trout fed almost entirely on bottom organisms.

Angling pressure and catch were concentrated in the northern area and three effects of this unequal harvesting were (1) fewer trout in relation to food abundance, (2) large numbers of bottom organisms owing to lack of predation, and (3) movements of trout into the area.

Yellowstone Lake is oligotrophic and has a deep productive depth. The dominant species composition of plankton and bottom organisms has not changed from 1890 to the present. Low availability of small trout to anglers is caused by feeding habits and great dispersal; this serves to prevent overexploitation of small trout.

LITERATURE CITED

Ayers, John C., David C. Chandler, George H. Lauff, Charles F. Powers, and E. Benette Henson.

1958. Currents and water masses in Lake Michigan. Great Lakes Research Institute, University of Michigan, Publication No. 3. 169 pp.

Ball, Orville P.

1955. Some aspects of homing in cutthroat trout. Utah Academy of Sciences, Arts, and Letters, Proceedings, vol. 32, pp. 75–80.

Ball, Robert C., and Don W. Hayne.

1952. Effects of the removal of the fish population on the fishfood organisms of a lake. Ecology, vol. 33, No. 1, pp. 41–48.

Ball, Orville P., and Oliver B. Cope.

1961. Mortality studies on cutthroat trout in Yellowstone Lake. U.S. Fish and Wildlife Service, Research Report 55.

Bauer, C. Max.

1955. Yellowstone, its underworld. University of New Mexico Press, Albuquerque, N. Mex. 118 pp.

Calhoun, A. J.

1944a. The bottom fauna of Blue Lake, California. California Fish and Game, vol. 30, No. 2, pp. 86–94.

1944b. The food of the black-spotted trout (*Salmo clarkii henshawi*) in two Sierra Nevada lakes. California Fish and Game, vol. 30, No. 2, pp. 80–85.

Carruthers, J. N.

1958a. A leaning-tube current indicator "Pisa." Institute of Oceanography, Monaco, Bulletin No. 1126. 34 pp.

1958b. Seine net fishermen can easily observe bottom currents themselves. The Fishing News, London, July 25, 1958, pp. 6–7.

Cope, Oliver B.

1956. Some migration patterns in cutthroat trout. Utah Academy of Sciences, Arts, and Letters, Proceedings, vol. 33, pp. 113–118.

1957. The choice of spawning sites by cutthroat trout. Utah Academy of Sciences, Arts, and Letters, Proceedings, vol. 34, pp. 73–79.

Church, Phil E.

1945. The annual temperature cycle of Lake Michigan. II. Spring warming and summer stationary periods, 1942. University of Chicago, Department of Meteorology, Miscellaneous Report 18. 100 pp.

Echo, John B.

1956. Some ecological relationships between yellow perch and cutthroat trout in Thompson Lake, Montana. American Fisheries Society, Transactions, vol. 84, pp. 239–249.

Edmondson, W. T., G. C. Anderson, and Donald R. Peterson.

1956. Artificial eutrophication of Lake Washington. Limnology and Oceanography, vol. 1, No. 1, pp. 47–53.

FORBES, S. A.
1893. A preliminary report on aquatic invertebrate fauna of the Yellowstone National Park, Wyoming, and the flathead region of Montana. U.S. Fish Commission, Bulletin for 1891, vol. 11, pp. 207–256.

HUTCHINSON, G. EVELYN.
1957. A treatise on limnology. Vol. 1, Geography, Physics, and Chemistry. John Wiley & Sons, New York. 1,015 pp.

IRVING, ROBERT B.
1956. Ecology of the cutthroat trout in Henrys Lake, Idaho. American Fisheries Society Transactions, vol. 84, pp. 275–296.

JOHNSON, JAMES H.
1958. Surface-current studies of Saginaw Bay and Lake Huron. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries, No. 267. 84 pp.

LAAKSO, MARTIN and OLIVER B. COPE.
1956. Age determination in the Yellowstone cutthroat trout by the scale method. Journal of Wildlife Management, vol. 2, No. 2, pp. 138–153.

LUNDBECK, JOHANNES.
1934. Uber den "Primar Oligotrophen" Seetypes and Wollingster See als dessen mitleleuro paichen vertreter. Archiv for Hydrobiologie, vol. 27, No. 2, pp. 221–250.

MCCONNELL, WILLIAM J., WILLIAM J. CLARK, and WILLIAM F. SIGLER.
1957. Bear Lake, its fish and fishing. Utah State Department of Fish and Game, Idaho Department of Fish and Game, Wildlife Management Department of Utah State Agricultural College, 76 pp.

MCMAHON, V. H.
1954. Abundance and distribution of entomostracan plankton at Lakelse Lake, B. C., 1949–1952. Fisheries Research Board of Canada, Journal, vol. 11, No. 4, pp. 479–499.

MILLER, F. GRAHAM.
1952. Surface temperatures of the Great Lakes. Fisheries Research Board of Canada, Journal, vol. 9, No. 7, pp. 325–376.

MOORE, H. L., O. B. COPE, and R. E. BECKWITH.
1952. Yellowstone Lake trout creel censuses, 1950–1951. U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries, No. 81. 41 pp.

MORTIMER, C. H.
1952. Water movements in lakes during summer stratifications: evidence from the distribution of temperature in Windermere. Royal Society of London, Philosophical Transactions, Series B, Biological, vol. 236, pp. 355–404.

OHLE, W.
1955. Ionen austausch der Gewassersedimente. Memorie Istituto Italiano Idrobiol. de Marchi, Suppli, vol. 8, pp. 221–248.
1956. Bioactivity, production, and energy utilization of lakes. Limnology and Oceanography, vol. 1, No. 3, pp. 139–149.

PENNAK, ROBERT W.
1955. Comparative limnology of eight Colorado mountain lakes. University of Colorado Studies, Series in Biology, vol. 2, p. 75.
1957. Species composition of limnetic zooplankton communities. Limnology and Oceanography, vol. 2, No. 3, pp. 222–232.

RAWSON, D. S.
1953. The bottom of Great Slave Lake. Fisheries Research Board of Canada, Journal, vol. 10, No. 8, pp. 486–520.
1955. Morphometry as a dominant factor in the productivity of large lakes. International Association of Theoretical and Applied Limnology, Proceedings, vol. 12, pp. 164–175.

REIMERS, NORMAN.
1958. Conditions of existence, growth, and longevity of brook trout in a small, high-altitude lake of the eastern Sierra Nevada. California Fish and Game, vol. 44, No. 4, pp. 319–333.

REIMERS, NORMAN, JOHN A. MACIOLEK, and EDWIN P. PISTER.
1955. Limnological study of the lakes in Convict Creek Basin. Mono County, California. U.S. Fish and Wildlife Service, Fishery Bulletin, No. 103, vol. 56, pp. 437–503.

ROBERTSON, J. G.
1954. The trophic status of Port John Lake, British Columbia. Fisheries Research Board of Canada, Journal, vol. 11, No. 5, pp. 624–651.

RODHE, W.
1949. The ionic composition of lake waters. Verh. Int. Ver. Limnol., vol. 10, pp. 377–386.

ROELOFS, EUGENE W.
1944. Water soils in relation to lake productivity. Michigan State College, Agricultural Experiment Station, Technical Bulletin 190. 31 pp.

THIENEMANN, A.
1928. Der Sauerstoff im eutrophen und oligotrophen Seen. Die Binnegewasser, 4. Stuttgart, Schweizerbartsche Verlagsbuchhandlung. 175 pp.

TONOLLI, VITTORIO.
1954. Stabilita E Produttivita del Limnobio Alpino. Memorie Istituto Italiano Idrobiol., vol. 8, pp. 29–70.

U. S. GEOLOGICAL SURVEY.
1952. Surface water supply of the United States, Part 6–A. Missouri River Basin above Sioux City, Iowa. U.S. Geological Survey, Water Supply Paper No. 1239. 450 pp.
1953. Surface water supply of the United States, Part 6–A. Missouri River Basin above Sioux City, Iowa. U.S. Geological Survey, Water Supply Paper No. 1279. 458 pp.
1954. Surface water supply of the United States, Part 6–A. Missouri River Basin above Sioux City, Iowa. U.S. Geological Survey, Water Supply Paper No. 1339. 381 pp.
1955. Surface water supply of the United States, Part 6–A. Missouri River Basin above Sioux City, Iowa. U.S. Geological Survey, Water Supply Paper No. 1389. 423 pp.

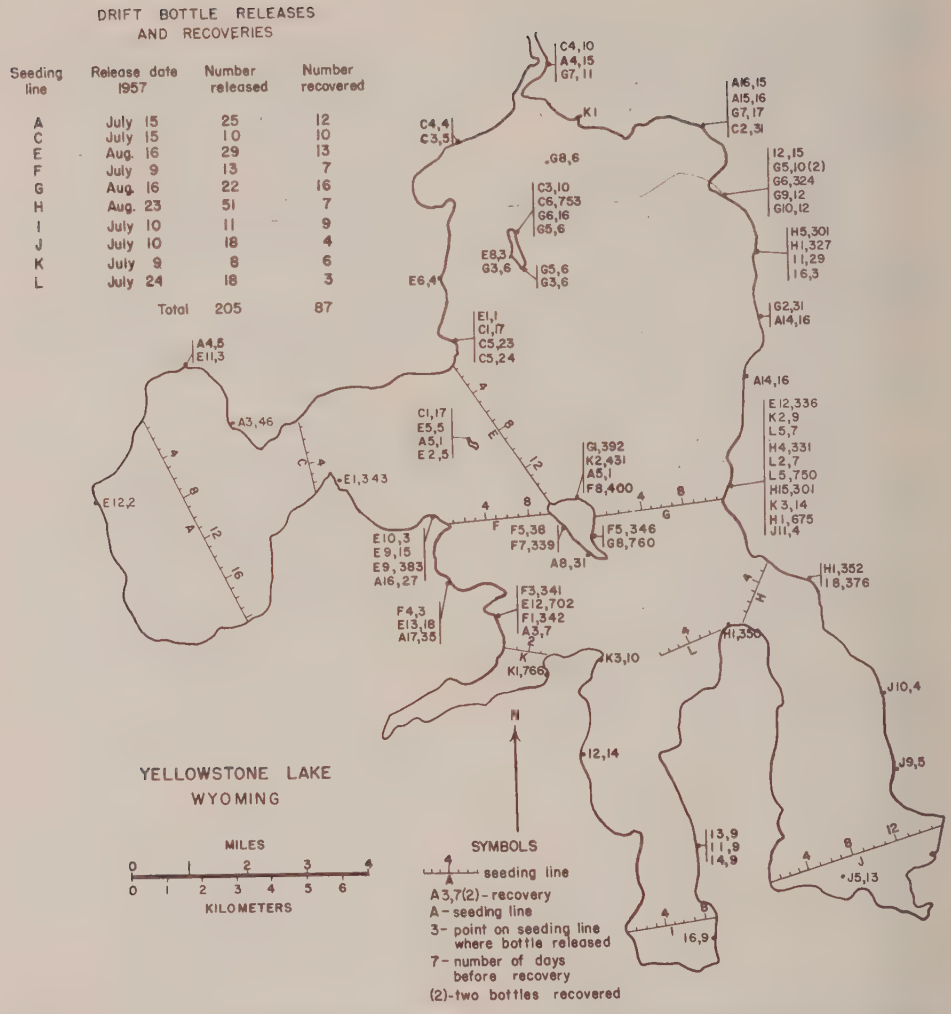
U.S. PUBLIC HEALTH ASSOCIATION, INC.
1955. Standard methods for the examination of water, sewage, and industrial wastes, 1955. Tenth edition. 522 pp.

WARD, JAMES.
1955. A description of a new zooplankton counter. Quarterly Journal of Microscopical Science, vol. 96, No. 3, pp. 371–373.

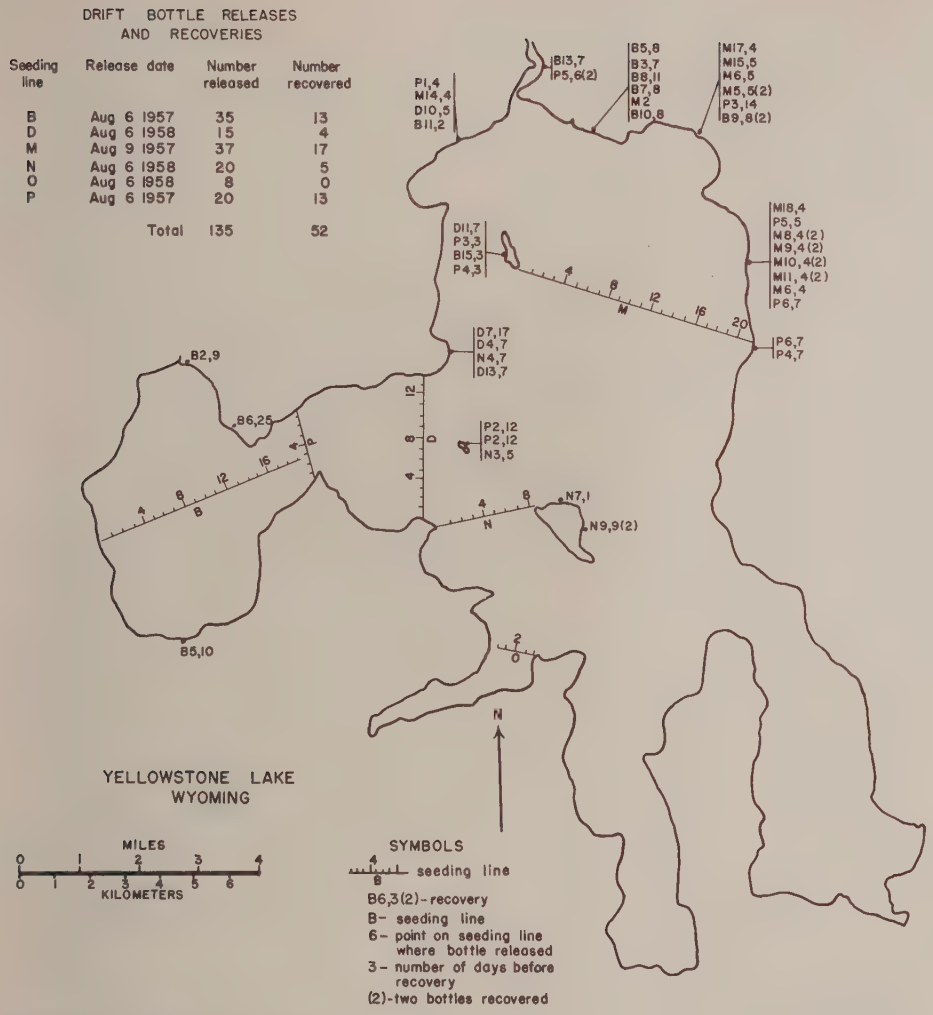
WELCH, PAUL S.
1948. Limnological Methods. Blakiston Co., Philadelphia. 381 pp.

WISLER, C. O. and E. F. BRATER.
1949. Hydrology. John Wiley & Sons, New York. 419 pp.

WOHLSCHLAG, DONALD E.
1950. Vegetation and invertebrate life in a marl lake. Investigations of Indiana Lakes and Streams, vol. 3, No. 9, pp. 321–372.


DRIFT BOTTLE RELEASES AND RECOVERIES
Seeding line | Release date 1957 | Number released | Number recovered
A | July 15 | 25 | 12
C | July 15 | 10 | 10
E | Aug. 16 | 29 | 13
F | July 9 | 13 | 7
G | Aug. 16 | 22 | 16
H | Aug. 23 | 51 | 7
I | July 10 | 11 | 9
J | July 10 | 18 | 4
K | July 9 | 8 | 6
L | July 24 | 18 | 3
Total 205 87
YELLOWSTONE LAKE
WYOMING
MILES
KILOMETERS
N
SYMBOLS
seeding line
A3,7(2) - recovery
A - seeding line
3 - point on seeding line where bottle released
7 - number of days before recovery
(2) - two bottles recovered

Appendix A.—Points of release and recovery of drift bottles in Yellowstone Lake, Wyoming.



APPENDIX B.—Points of release and recovery of drift bottles in Yellowstone Lake, Wyoming.

U. S. GOVERNMENT PRINTING OFFICE : 1962 O - 595956